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**MEASUREMENTS AND ANALYSIS OF
EYE MOVEMENTS AND THEIR ROLE IN
THE PROCESS OF VISUAL BRIGHTNESS PERCEPTION**

H. P. W. STASSEN

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MEASUREMENTS AND ANALYSIS OF EYE MOVEMENTS AND THEIR ROLE IN THE PROCESS OF VISUAL BRIGHTNESS PERCEPTION

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HENRICUS PETRUS WILHELMUS STASSEN

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Aan Vader en Moeder,
Toos,
Rik en Peter.

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GENERAL INTRODUCTION

As a result of the eye movements, with respect to the surroundings, which are always present the retinal image of a stationary target is never completely fixed upon the retina in normal vision.

The question to what extent these movements of the retinal image significantly affect the process of visual perception is of fundamental interest. Two kinds of experimental evidence are especially relevant in regard to this question, viz. first, detailed quantitative data of eye movements under a well defined viewing condition and instruction of the observer and, second, experiments on vision in which a stabilized image is moved with previously recorded eye movement signals or components of these signals.

During some decades the effects of image stabilization were investigated and experiments were carried out concerning the influences of motion imposed on stabilized images in the Laboratory of Medical Physics and Biophysics (Gerrits et al. 1970a; 1970b; 1974; 1978).

This thesis deals with the precise measurements and analysis of eye movements in order to investigate their role in the process of visual perception, in particular the generation and maintenance of brightness perception.

In chapter 1 the measuring system used and the eye movements recorded during the observation of differently sized bright squares are described for different subjects. The results obtained show that the size of the eye movements increases with the size of the observed square, which is mainly due to an increase of the saccade amplitudes and frequencies. The changes in the drifts with increasing square size are not very marked and therefore seem to play a minor role in brightness perception for larger squares.

In chapter 2 the correlation between the saccades and drifts in the movements of the two eyes during binocular fixation on a small fixation target was investigated. A rather strong correlation of the saccades as well the drifts in the two eyes was found under these conditions.

In chapter 3 the effects of imposed retinal image movements on the process of visual perception was investigated. Thereby the influences of the subject's own eye movements are annulled by means of stabilization. For a bright square with sides of four degrees the influences of saccades and drifts, separately and together, have been investigated for two subjects. The results show that both subjects with their imposed saccades are provided with a perception of approximately the same quality as obtained during the unstabilized observation of the same stimulus. This perception improved either nothing or just a little on the addition of their drift movements. However, for the effectiveness of their drifts we observed a striking difference between the two subjects. In spite of the drift amplitude of subject H.G. being markedly smaller, this drift provided him with a better quality of perception than subject H.S. obtained with his larger drift movements. For subject H.G. the effectiveness of his saccades and drifts is about equal, whereas for subject H.S. saccades are more effective than his drifts.

The drifts alone are found to be sufficient to provide for the maintenance of foveal perception. Because of the low rate of the small saccades during foveal observation, these small saccades alone are probably unfitted to preserve foveal perception. We conclude that for small targets observed with the fovea the drifts are sufficient, for large targets the saccades are sufficient, while for the intermediate range of target sizes the saccades and drifts both contribute for the perception of brightness.

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EYE MOVEMENTS DURING OBSERVATION OF DIFFERENTLY SIZED SQUARES

1.1 Introduction

There are several possible ways of interpreting eye movements made by a subject in a stationary environment.

One way is to regard saccades as eye movements which allow the visual system to use the most specialised retinal area, the fovea, to process detailed visual information in successive fixations. Many studies have shown the saccadic nature of eye movements during the observation of complex objects (e.g. Yarbus 1967). Two to three saccades per second is typical. In the intersaccadic intervals only a small amplitude movement persists. If instead of complex objects a small fixation target was observed while efforts were being made to keep the eye on that particular target, small involuntary eye movements would occur. These involuntary eye movements contain small saccades. In the intersaccadic intervals the eye drifts about slowly and haphazardly. A very small, irregular oscillation, called tremor, has been observed in very sensitively recorded eye movements to be superimposed on this intersaccadic drift movement. In fixational eye movements too, the small saccades occur typically two to three times per second. (For a general review of properties of fixational eye movements see Ditchburn, 1973.)

Further insight into the role of eye movements has been gained by investigation of stabilized images (e.g. Yarbus, 1967; Gerrits et al., 1966; 1970a). The perception of a well stabilized retinal image disappears within a few seconds, showing the need for eye movements in normal vision for maintaining visual perception.

The adequacy of various movements for the maintenance of vision has been studied in our laboratory by imposing motion on stabilized images (e.g. Gerrits and Vendrik, 1970b; 1974). By imposing a variety of types of movements on a centrally fixated white square (of 4 degrees side) results were obtained suggesting that movements which shift the image continuously and irregularly over the retina are necessary for normal continuous vision. Only

the drifts in eye movements possess both qualities, but an improvement of perception was obtained by the addition of small saccades. These studies also showed that eye tremor is unlikely to be of any significance in this regard, because of both its small amplitude and its spectral characteristics.

Steinman et al. (1967; 1973) showed that saccades in fixational eye movements could be suppressed for up to 10 seconds or more by practised observers without any reduction in the accuracy of fixation and without loss of perception of the foveal fixation target, again indicating the effectiveness of drifts in maintaining a foveal perception.

We wish to investigate which properties of eye movements are essential for the maintenance of vision under normal conditions. The literature reveals a lack of good quantitative data for eye movements during the observation of square stimuli of the kind used by Gerrits and Vendrik (1974). Because the structure of the retina is such that receptive fields increase in size with increasing eccentricity, larger eye movements are probably needed to activate the receptive fields near the borders of larger targets. Literature likewise fails to provide a good description of the possible changes in the properties of saccades and drifts as the size of the observed target is varied from very small to larger dimensions. Therefore the eye movements in normal vision were studied during the observation of square stimuli of different size. Also some experiments were performed while subjects were observing a target of 4 degrees side length with different brightnesses.

According to Listing's law (Duke Elder, 1961) torsional motions of the eyeball about the visual axis are very small in comparison with the horizontal and vertical components of eye movements. Because of this and also for other practical reasons only the horizontal and vertical components were measured in the experiments described.

The results show that the size of eye movements increases with the size of the observed target. This is mainly due to an increase of the saccade amplitudes and frequencies, while the changes in the amplitudes of drifts and tremor are not very marked. This indicates that while drifts may be sufficient for

normal vision of small foveal targets, increasing saccade size and probably also saccade frequency gain importance for maintaining normal vision when the visual system has to deal with large stimuli. The influence of the brightness of a target with sides of 4 degrees on the properties of the drifts is not very marked. A marked influence can be observed in the occurrence of a smaller mean saccade magnitude with increasing brightness of the stimulus.

1.2 Methods

After thorough comparison of the methods available for the precise measurements of eye movements we opted for the method described by Robinson (1963). In his set-up a search coil is attached to the eye and placed in two perpendicularly alternating electromagnetic fields in phase quadrature. Eye movements could be recorded very accurately by measuring the induced voltages in the search coil.

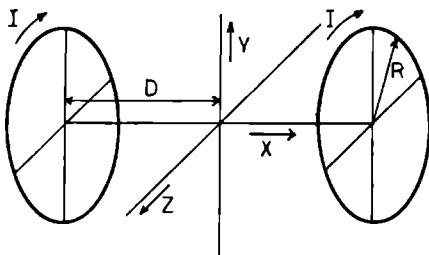
In our measurement system a search coil, attached to the subject's eye, is positioned accurately in the centre of an open frame support carrying two pairs of field coils. Each coaxial pair creates a uniform field at the position of the search coil. One pair is situated on the subject's left and right and creates a medial-lateral magnetic field B_x in the x-direction. The other pair is situated above and below (girdling the neck) and creates a rostral-caudal magnetic field B_y in the y-direction. In the primary position of gaze the search coil lies parallel to both field directions and no voltages are induced. As the eye turns nasally or temporally the search coil intercepts flux from the B_x field and the induced voltage with the frequency of the x-field records the extent of the horizontal movement. As the eye makes vertical movements the search coil intercepts flux from the B_y field and the induced voltage with the frequency of the y-field records the extent of the vertical movement. In contrast with Robinson (1963) who used equal frequencies for the x-y-fields of about 4.5 kHz, which were 90 degrees out of phase of each other, we preferred different frequencies of about 30 kHz and 20 kHz respectively for the horizontally and verti-

cally directed fields. In this way measurement errors resulting from possible phase errors between the two fields were prevented. Another advantage is that the measurement system is inaudible with the use of these higher frequencies. To calibrate the sensitivity of the measurement system the amplitudes of the electromagnetic fields were adjustable. To minimize measurement errors caused by possible changing amplitudes of the fields, the fields were stabilized. The voltage induced in a secondary coil wound around the field coils was used for stabilizing the measurement system. The voltages induced in the search coil during eye movements were detected by means of two lock-in amplifiers (Princeton Applied Research, model 128A). each locked to one of the field frequencies.

1.2.1 Calculations for the design of the measurement system

According to Biot and Savart the amplitude of the magnetic induction generated in the centre of the axis which connects the centers of the two parallel situated field coils (see fig.1.1) caused by an equal amplitude alternating current is:

$$B_x(\bar{O}) = \mu_0 \cdot N \cdot I \cdot \frac{1}{(1 + K^2)^{3/2} \cdot R} \quad (\text{Wb/m}^2) \quad (1)$$



$B_x(\bar{O})$ = amplitude of the magnetic induction in the centre

μ_0 = permeability of free space

R = radius of field coils

D = distance from the centre to the plane of the field coil

N = number of turns on each coil

I = amplitude of the electric current in each coil

K = D/R ratio

Fig.1.1 The configuration of the pair of field coils generating the electromagnetic field in the x-direction.

Robinson (1963) showed that the rate at which $B_x(\bar{0})$ changes as one moves a distance δ along the x-axis or off the x-axis is minimized under the condition:

$$R \approx D \quad (2)$$

The error in the field uniformity (first order approximation) is then given by:

$$\frac{B_x(\delta) - B_x(\bar{0})}{B_x(\bar{0})} = \frac{9}{8} \left(\frac{\delta}{R} \right)^2 \quad (3)$$

Equation (3) shows that a large field coil radius reduces the effects of search coil displacements. According to equation (1) on the other hand the amplitude of the magnetic induction caused by a given current I diminishes with increasing radius R.

The amplitude of the induced voltage in a search coil positioned in the centre and inclined by an angle φ_x in the x-field is:

$$V_{s.c.} = n \cdot A \cdot B_x \cdot 2\pi \cdot f_x \cdot \sin \varphi_x \quad (4)$$

$V_{s.c.}$ = amplitude of the induced voltage

n = number of turns on the search coil

f_x = frequency of the x-field

The amplitude of the alternating current I is related to the amplitude of the voltage V_f over the two field coils connected in series, according to:

$$I = \frac{V_f}{4\pi \cdot f_x \cdot L} \quad (5)$$

I = amplitude of the electric current through the coils

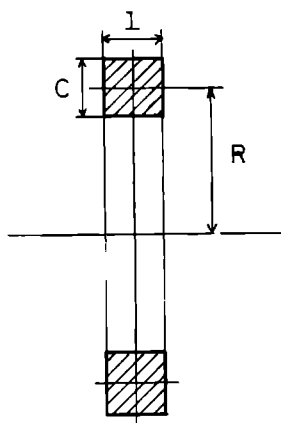
V_f = amplitude of the voltage over the two field coils connected in series

L = inductance of one field coil

In equation (5) the contribution of the mutual inductance, which measured in practice about 0.3 percent of the inductance of each pair of field coils, has been neglected. Also the capacitance and resistance of the coils have been neglected.

The inductance L of a field coil can be calculated by an empiric formula (Meinke, M. and Fundlach, F.W., 1962) according to:

$$L = \frac{312 \cdot N^2 \cdot R}{6 + 9q + 10p} \cdot 10^{-7} \text{ (H)} \quad (6)$$



N = number of turns on the field coil

$q = l/R$ ratio

$p = C/R$ ratio

R = radius of the field coil (m)

Fig.1.2 The dimensions of the field coil.

Substitution of (6), (5) and (1) in (4) gives:

$$V_{s.c.} = \pi \cdot \frac{6 + 9q + 10p}{156} \cdot \frac{1}{(1 + K^2)^{3/2} \cdot R^2} \cdot \frac{n}{N} \cdot A \cdot V_f \cdot \sin \varphi_x \quad (7)$$

Equation (7) shows a relation between the amplitude of the voltage V_f over the field coils and the amplitude of the induced voltage in the search coil $V_{s.c.}$ when the search coil is inclined by an angle φ_x with respect to the x-field.

In practice the voltage V_f is obtained by means of resonance. Therefore the two field coils are connected in series with a capacitor and driven by an amplifier. Stabilization and regulation of the amplitude of the voltage V_f and the maintenance of oscillating conditions were realized by means of an electronic circuit.

In fig.1.3 a simplified replacement scheme for the oscillating circuit is shown.

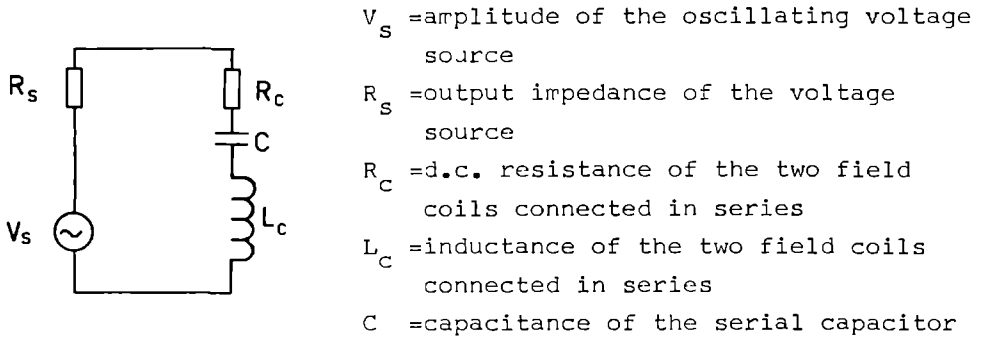


Fig.1.3 A simplified electronic replacement scheme for the magnetic field system.

The circuit oscillates at the frequency ω_0 according to:

$$\omega_0 = \frac{1}{\sqrt{L_c \cdot C}} \quad (\text{rad. s}^{-1}) \quad (8)$$

For the tuned frequency ω_0 the amplitude of the voltage V_f is related to the voltage V_s according to:

$$V_f = Q_t \cdot V_s \quad (9)$$

Q_t represents the total quality factor of the oscillating circuit. Q_t can be calculated according to:

$$Q_t = \frac{\omega_0 \cdot L_c}{R_s + R_c} \quad (10)$$

In order to obtain a relatively high value for Q_t we might choose a relatively high frequency ω_0 in combination with a relatively high inductance L_c and a small $(R_s + R_c)$ value. However, in practice we found the occurrence of a maximal value for Q_t which was limited by the characteristics of our amplifier functioning as voltage source. Especially R_s was found to increase for frequencies above 20 kHz. Therefore we found a maximum value for

Q_t at about 20 kHz remaining at about this maximum value up to about 30 kHz and decreasing above this frequency. Also an increase of the number of turns N on the field coils finally did not result in higher values for Q_t .

According to equation (7) with a given amplitude V_f and fixed search coil dimensions the sensitivity is optimized especially by choosing a small radius R for the field coils. According to equation (7) one might also gain sensitivity by reducing the number of turns N on the field coils. However, reducing the number of turns N is restricted by the practical limitations of the amplifier used to deliver electric current to the field coils. After some preliminary experiments we chose the following practical dimensions for our field coils forming the magnetic field cube.

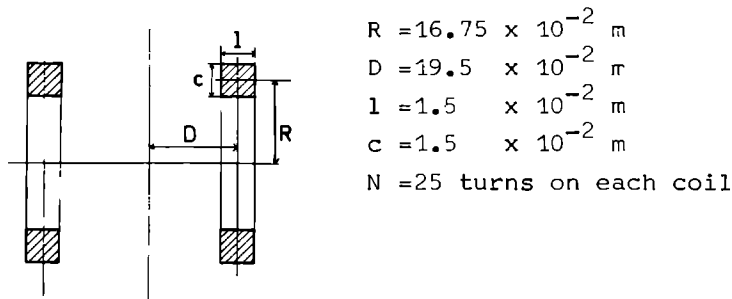


Fig.1.4 The configuration of the field coils for the generation of one field.

In order to accommodate the subject's head, the radius of the coils forming the magnetic field cube was chosen $16.75 \times 10^{-2} \text{ m}$. We used insulated copper wire, diameter $1.4 \times 10^{-3} \text{ m}$, with a rather thick isolation measuring $0.7 \times 10^{-3} \text{ m}$. This was found advantageous in regard to minimizing the parallel capacity formed between the layers of wire forming the field coils. The amplitude of the voltage V_f could be regulated. A maximal value of about 280 volts, corresponding to a magnetic field strength in the centre of about $1.4 \times 10^{-4} \text{ Wb/m}^2$, could be obtained. The stabilization of V_f was measured. During one hour of operation the amplitude drift was smaller than 0.3 percent. Also the homogeneity of the fields was measured and found in

good accordance with the predictions from equation (3).

A maximal value for Q_t of about 55 was obtained in the frequency range from 20 to 30 kHz. Therefore we chose 20 and 30 kHz for the vertically and horizontally directed fields respectively. In choosing these high frequencies there was also the advantage of getting an inaudible measuring system.

1.2.2 The eye attachments

For the measurements of the horizontal and vertical components of eye movements a search coil was attached to one of the moving eyes. The search coil had a radius of 8.8×10^{-3} m and consisted of 10 turns of insulated copper wire with a diameter of 5×10^{-5} m. Two kinds of eye attachments were available for this purpose, a silicone eye coil and a suction cap. The silicone eye coil was made of a silicone rubber annulus in which a search coil was imbedded (Collewijn et al., 1975). When the silicone eye coil was pressed against the sclera, without touching the cornea, it was sucked to it by the elastic deformation forces in the rubber. To ensure firm suction, particular care has to be taken to press all the air and fluid away from beneath the annulus. The eye was previously anaesthetised with Novesine (0.2 per cent). Because of the anaesthesia the blink reflex was not as active as in normal vision, the more so because the other eye was closed and covered with a cloth. When a silicone eye coil was used this could cause drying-out of the cornea, resulting in poor vision. To prevent this effect the subject was instructed to blink deliberately at regular intervals. The visual acuity of the subject was checked regularly during the experiments. A suction cap normally used for stabilizing retinal images (Gerrits et al., 1966) was equipped with a holder for a search coil. To enable normal vision the lens was replaced by flat glass. The artificial pupil measured 4×10^{-3} m in diameter. Heated water flowing around the cap prevented the glass from becoming covered with moisture. The cap was sucked firmly against the eyeball by means of an underpressure of about 5×10^3 Pa. The closed chamber construction of the suction cap prevented the

cornea from drying-out.

The mass of the suction cap measured 1.8×10^{-3} kg, which was large in comparison with the 0.1×10^{-3} kg mass of the silicone eye coil.

The transducers should fulfill two conditions: during eye movements the transducers should keep the same position with respect to the eyeball, and normal eye movements should not be hampered to an appreciable extent by the transducers.

As Collewijn et al. (1975) we did not find any evidence for suspecting the silicone eye coil of slipping or influencing the eye movements.

As a general rule the suction cap follows small eye movements correctly, as is proved by the experiments with stabilized images (Gerrits et al., 1966), although the eyelids probably cause friction against this eye attachment. Results obtained with the measurements of binocular eye movements (chapter 2) showed that in situations where one eye was equipped with a silicone eye coil and the other with a suction cap, the suction cap lowered the eye mobility by about 20 per cent. This lowered eye mobility was not caused by slipping of the cap but by additional friction on the cap due to the eyelids.

Therefore in the experiments described in chapter 1 all subjects used a silicone eye coil during the measurement of their eye movements.

1.2.3 The characteristics of the measurement system

The frequency response of our measurement system is flat from 0 Hz up to 220 Hz (-3 dB). In the measurement range of 300 min.arc, the range most often used, the r.m.s. value of the noise measured 3 sec.arc, corresponding to a peak to peak value of about 18 sec.arc.

During the experiments the search coil was located in the most homogeneous central area of the magnetic field cube. Within a small cube of 1.5×10^{-2} m side around the centre the homogeneity of the fields was better than 99 percent. With the aid of a suction pillow the head was immobilized in the position in which the search coil on the eye was in that homogeneous part of the

fields. The suction pillow also helped to minimize the head movements. In a preliminary experiment the head movements were measured by attaching a search coil to the teeth of the subject's upper jaw. Recordings indicated that the range of head movements, when the suction pillow was used, measured about 2 to 3 min.arc. which is small in comparison with eye movements.

1.2.4 The recording system

To exclude high-frequency noise generated in the measuring system, the eye movement signals were filtered with a steep low-pass filter (Krohnwhite type 3343; 180 Hz - 1.5 dB down; 48 dB/octave; RC mode).

In our first experiments the measured eye movements were recorded on a four channel F.M. tape recorder (Hewlett and Packard type 3960). In the measurement range of 300 min.arc, the range most often used, the peak to peak noise level in the replayed signals measured 45 sec.arc.

During the second half of this research project we had at our disposal a 12-bit pulse-code modulated recorder system (Kaiser, Munich), enabling four channels to be recorded simultaneously at a rate of 500 samples per second for each channel. When this recorder system was used, the peak to peak noise level in the replayed signals was cut down to about 20 sec.arc.

1.2.5 The analysis of the recorded eye movements

The recorded eye movements were analysed with the aid of a digital computer (PDP 11/45). To exclude possible high-frequency noise introduced by the tape recorder the replayed eye movements were filtered before sampling. Again a steep low-pass filter was used (Krohnwhite type 3343; 180 Hz - 1.5 dB down; 48 dB/octave; RC mode).

The horizontal and vertical eye movement signals were stored on disk at a rate of 400 samples per second for each channel and an accuracy of 12 bits. It was possible to store up to 180 consecutive seconds of eye movements in one file. In order to analyse the saccadic and intersaccadic components of the eye movements the moments of the onset and offset of saccades and

blink-associated eye movements (referred to as "blinks" for short) had to be detected. Their velocities are greater than those of drifts and tremor. The moment of onset of a saccade or blink was detected when a threshold velocity in either the horizontal or the vertical signal was exceeded for a minimum number of consecutive samples (e.g. 3). The threshold velocity was usually 200 min.arc per second. The first moment of sampling when this occurred was defined as the moment of onset of a saccade or blink and the moment of offset of the previous drift and tremor movement. Similarly, the offset of a saccade or blink and the onset of the next drift and tremor movement was detected when the eye velocity dropped below the threshold for a certain minimum period of time (e.g. 8 sample intervals).

Detection of the moments of onset and offset of saccades and blinks was visually controlled on the computer display. In some cases when a few small saccades were missed the threshold velocities and the associated time windows (see above) were changed until all saccades and blinks had been detected correctly. In our experiments almost all saccades lasted less than 60 ms. Blinks usually lasted longer and were rejected from further analysis on that basis.

The main possibilities of our software programs for the analysis of the recorded eye movements were as follows:

1. The production of plots on the computer display showing the horizontal and vertical components against time and against each other. These plots were used to inspect the recorded eye movements.
2. The calculation of the standard deviations of the horizontal and vertical components as a measure for the size of eye movements. This standard deviation was calculated according to:

$$\sigma = \sqrt{\frac{\sum_{i=1}^{n-1} (x_i - \bar{x})^2}{n - 1}} \quad \text{with: } \bar{x} = \sum_{i=1}^n \frac{x_i}{n}$$

x_i = the horizontal or vertical position at the moment i ,
 n = the total number of horizontal or vertical samples in the file. Normally a file measured 180 s corresponding to

$n = 72000$. Experimentally we found that starting the calculation of $\sum_{i=1}^{n-1} (x_i - \bar{x})^2$ with a running average $\bar{x} = \sum_{i=1}^n \frac{x_i}{n}$ gave approximately the same results as calculating first \bar{x} and thereafter using this mean value.

3. The calculation of saccade characteristics. Therefore the distances of the saccade positions at the moments of onset and offset were calculated. From these displacements histograms were compiled and mean values and standard deviations calculated. The vectorial magnitudes were determined from the horizontal and vertical magnitudes.
4. The determination of the durations of the drifts (the intersaccadic intervals). Histograms of these drift durations were plotted and the mean drift duration and standard deviation were calculated.
5. The calculation of the effective displacements of the drifts. Because the movement of the eye during any intersaccadic interval usually looked like a linear movement with superimposed small irregularities the effective displacements of the drifts were calculated by comparison of the eye positions at the moments of onset and offset of the intersaccadic intervals. Of these effective displacements histograms were plotted and mean values and standard deviations were calculated.
6. The calculation of the mean drift vector velocity. Computer analysis in which drift and tremor movements were investigated showed that mainly the low frequencies up to about 5 Hz contribute to the drifts. The higher frequencies have amplitudes smaller than 1 min.arc. This accords well with the established properties of tremor (see Ditchburn, 1973). The drift velocities were estimated by sampling drifts at 0.1 second time intervals, so that frequencies up to about 5 Hz contributed to the calculated velocity. Winterson and Robinson (1974) also have used time intervals of 0.1 and 0.2 seconds for the estimation of drift velocities.

1.3 Experiments and instructions

During the experiments the subject was supine with his head placed in the magnetic field cube. Before each session the subject's head was positioned accurately in order to locate the eye in the most homogeneous central area of the field cube.

White square stimuli, generated on a television screen, were observed by the subject via a mirror. The distance from the eye to the screen was 1.82 m. The brightness of the stimulus could be varied up to about 600 cd/m². In our experiments the brightness of the background was always varied proportional to the stimulus brightness giving a constant contrast.

In our experiments the contrast C was calculated according to:

$$C = \frac{B_{\max.} - B_{\min.}}{B_{\max.} + B_{\min.}} \quad \text{with:} \quad \begin{array}{l} B_{\max.} = \text{the maximum brightness} \\ B_{\min.} = \text{the minimum brightness} \end{array}$$

Three subjects (J.B.; G.P.; H.S.) were participating in the experiments in which they observed differently sized squares. They observed white squares with sides varying from 15 up to 240 or 450 min.arc. The brightness of the squares in these experiments was always 150 cd/m², while the background was about 3 cd/m² giving a contrast $C = 0.96$.

Preliminary experiments showed the ability of these subjects to cause fading of the periphery by limiting their eye movements while observing a particular square (Troxler's effect; Troxler, 1804). For squares with sides exceeding about two degrees of arc complete fading was occasionally reported when saccades were suppressed.

We wanted to measure eye movements which were just sufficient for the maintenance of a satisfactory percept of the particular square observed. When a subject kept his eye movements too small, wide on and off borders near the contours of the square were clearly perceived. To ensure the minimal eye movements needed to maintain a satisfactory percept the subjects were instructed to look in the direction of the surmised centre of the square and to restrict their eye movements to a size such that on and off borders near the contours of the square were perceived only occasionally (see also Gerrits and Vendrik, 1970b and 1974).

While the subject observed a particular square, his eye movements were measured for about 210 seconds, of which the last 180 seconds were analysed.

In a second series of experiments subject H.G. and H.S. investigated the influence of the brightness of the stimulus with sides of 4 degrees of arc on the eye movements. The brightnesses used were 150; 27 and 5 cd/m^2 , while the contrast was kept constant ($C = 0.96$). In this second series of experiments we instructed the subjects to restrict their eye movements in order to give a percept according to one of the following descriptions:

Instruction 1

I1----- A percept of a square with on and off borders and a brightness in the centre which is just lower than the on borders.

Instruction 2

I2----- A percept of a homogeneously bright square with occasionally on borders near the contours (off borders should not be perceived).

1.4.1 Results

In all three subjects (J.B.; H.S. and G.P.) the square size observed influenced the pattern of eye movements. Figures 1.5, 1.6 and 1.7 show about 18 seconds of horizontal and vertical eye movements for each of them, recorded while they were observing a square of the indicated size. In general the eye movements increased in size with increasing dimensions of the square. There are differences between the subjects with regard to the sizes of eye movements when they observed a particular square size. Subjects J.B. and G.P. produced larger eye movements than subject H.S. Figures 1.5, 1.6 and 1.7 indicate that the increases in eye movements are brought about mainly by the saccades, while the changes in the drifts seem to play a minor role.

In the following figures the horizontal eye movement signal is marked with H, a movement to the right is indicated upwards. The vertical eye movement signal is indicated with V, a movement

upwards is also indicated upwards. The movement starts on the left.

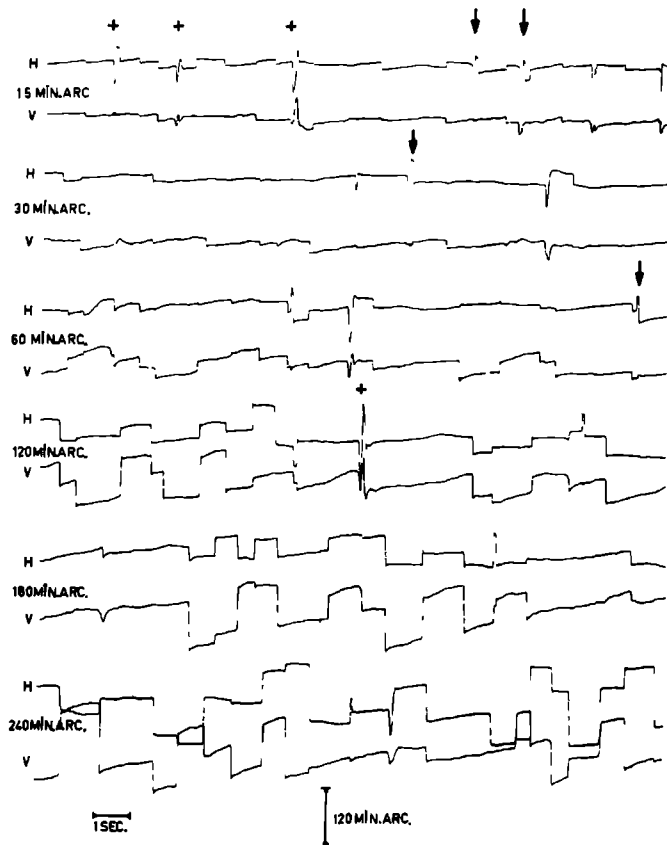


Fig. 1.5 Eye movements while looking at squares of the indicated length of side; subject J.B.
Some blinks are marked with crosses, while some double and triple saccades are marked with arrows.

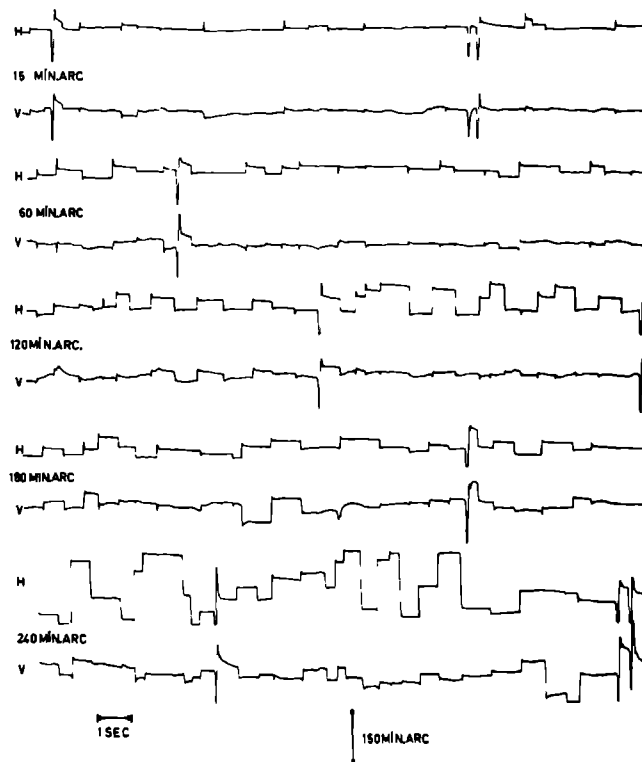


Fig. 1.6 Eye movements while looking at squares of the indicated length of side; subject G.P.

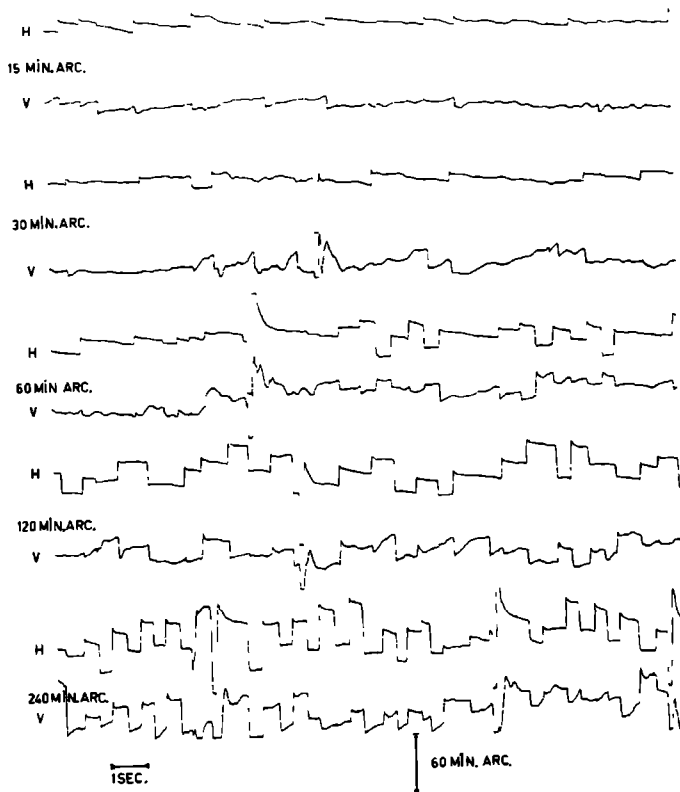


Fig. 1.7 Eye movements while looking at squares of the indicated length of side; subject H.S.

In figure 1.5 it is remarkable that during the observation of small sized squares double and triple saccades (indicated with arrows) occur, each consisting of two to three saccades in rapid succession. It is also noteworthy that the saccades made by subjects J.B. and H.S. (figures 1.5 and 1.7) show no overshoots. However, as can be seen from figure 1.6 the eye movements made by subject G.P. have saccades with quite marked overshoots; this was always observed with this subject.

In our view the presence or absence of overshoots depends on the subject.

Figure 1.8 shows in two-dimensional plots the eye movements of one subject during 180 seconds of observation of the squares of the indicated size. Similar two-dimensional plots were obtained for the other two subjects. The range of the trajectories for subject H.S. was markedly smaller.

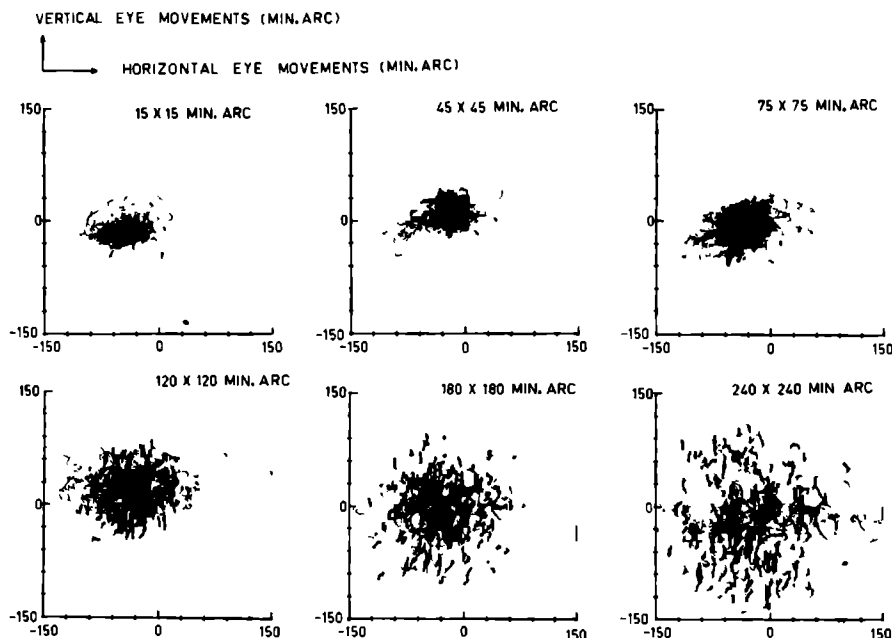


Fig. 1.8 Two-dimensional plots of eye movements, recorded during 180 seconds, as a function of square size, subject J.B. The (0,0) position corresponds to the middle of the measurement range, which is not necessarily the same as the centre of the observed square.

Various characteristics of eye movements as a function of square size are given in tables I, II and III for subjects J.B., G.P. and H.S., respectively.

The standard deviations of the horizontal and vertical components of eye movements are given as σ_h and σ_v , respectively. The mean and standard deviations of the drift and saccade magnitudes (min.arc) were calculated. The mode and maximal values were obtained from histograms. For the calculation of the drift durations (the intersaccadic intervals) a blink is counted as a saccade. The subjects, which used a silicone eye coil, normally blinked about every 8 seconds. The mean drift velocities were calculated over time intervals of 0.1 s in the drift periods.

Table I. Analyzed properties of eye movements as a function of square size.

Subject J.B.

square size	σ_h	σ_v	drift duration			saccade vector magni-				drift vector magni-				mean drift vec- tor velocity (min.arc/s)
	(min.arc)		(second)			tude (min.arc)				tude (min.arc)				
			mean (s.d.)	max.		mean (s.d.)	mode	max.		mean (s.d.)	mode	max.		
15'	6.7	4.9	0.76	0.64	2.9	18.8	13.1	10	70	7.9	5.0	7	27	16.6
30'	8.7	6.6	0.98	0.84	4.0	21.3	14.0	17	65	9.6	7.1	4	38	16.4
45'	7.6	10.7	0.85	0.72	4.2	23.3	13.2	18	81	9.9	7.4	10	34	16.4
60'	10.4	14.8	0.75	0.75	3.7	28.5	14.3	30	75	10.1	9.0	8	36	19.7
75'	15.0	17.1	0.75	0.64	3.6	35.6	15.0	29	80	10.1	8.2	8	42	20.4
90'	18.2	19.5	0.87	0.76	4.0	38.1	15.0	28	84	11.2	9.9	8	43	18.2
105'	19.7	17.8	0.81	0.84	5.1	41.9	15.3	41	81	10.7	9.2	9	44	19.4
120'	26.1	24.6	0.73	0.76	5.6	46.1	20.8	45	94	11.7	10.4	8	50	21.9
150'	30.8	27.6	1.07	0.93	7.5	59.0	20.8	58	118	14.2	11.4	9	50	17.9
180'	33.3	34.9	0.90	0.83	4.8	69.3	28.0	81	123	14.6	13.8	12	52	23.0
210'	39.6	36.1	0.75	0.64	3.5	65.4	27.5	64	135	12.7	10.1	11	50	22.9
240'	45.8	45.4	0.75	0.71	3.0	94.5	41.5	100	170	13.9	11.6	12	50	25.3

Table II. Analyzed properties of eye movements as a function of square size.

Subject G.P.

square size	σ_h σ_v (min.arc)		drift duration (second)			saccade vector magni- tude (min.arc)				drift vector magni- tude (min.arc)				mean drift vec- tor velocity (min.arc/s)
			mean (s.d.)max.			mean (s.d.) mode max.				mean (s.d.) mode max.				
15'	5.8	6.1	0.80	0.77	4.0	13.7	9.1	8	54	5.9	4.0	4	20	16.4
60'	11.6	11.4	0.61	0.42	2.3	18.0	13.2	20	91	5.6	4.5	3	29	17.8
120'	24.1	17.3	0.55	0.29	2.1	35.6	21.2	24	94	6.5	4.1	5	28	19.9
180'	26.2	21.5	0.54	0.34	2.9	41.4	28.7	25	151	6.3	4.6	5	36	20.4
240'	65.9	38.2	0.50	0.35	3.0	80.5	60.4	50	200	7.2	7.0	4	48	22.9

Table III. Analyzed properties of eye movements as a function of square size.

Subject H.S.

square size	σ_h σ_v		drift duration			saccade vector magnitude				drift vector magnitude				mean drift vector velocity
	(min.arc)		(second)			(min.arc)				(min.arc)				
			mean	(s.d.)	max.	mean	(s.d.)	mode	max.	mean	(s.d.)	mode	max.	(min.arc/s)
15'	4.7	7.5	1.25	1.25	6.1	8.6	4.2	6	27	9.2	7.3	7	28	20.3
30'	5.5	7.9	0.88	0.83	6.4	10.8	5.1	11	28	8.8	6.2	6	28	22.9
45'	7.8	10.7	1.00	0.88	6.3	11.9	6.8	7	42	8.1	5.6	5	30	22.2
60'	6.4	9.7	0.82	0.80	5.9	10.5	4.9	8	27	8.4	6.3	6	33	18.8
75'	10.1	13.4	0.76	0.67	5.2	12.5	7.0	10	42	9.9	8.4	5	38	21.6
90'	8.9	11.9	0.61	0.43	3.8	13.4	6.4	12	50	8.5	6.3	7	40	28.5
105'	11.1	10.6	0.59	0.43	3.2	16.9	9.5	14	60	7.3	5.4	5	38	23.0
120'	12.3	10.8	0.73	0.80	7.2	17.6	8.7	20	44	8.3	8.1	4	36	26.7
150'	13.6	12.0	0.57	0.31	2.0	19.8	12.4	15	80	6.4	5.0	4	32	19.4
180'	17.6	16.8	0.53	0.52	2.8	18.2	11.2	16	60	8.8	6.9	6	32	33.1
210'	15.1	15.2	0.49	0.26	1.8	22.4	12.6	22	84	8.1	8.1	6	32	28.7
240'	19.9	22.1	0.37	0.29	2.5	25.6	16.4	20	85	8.6	7.5	6	35	38.2
450'	29.1	33.0	0.38	0.19	1.5	41.9	23.0	27	150	9.0	5.9	7	32	32.4

1.4.2 The size of eye movements

For all subjects both the horizontal and vertical standard deviation increased with the size of the square.

The measured positions of the eye appeared to have approximately a bivariate normal distribution, where σ_h and σ_v are the standard deviations along the two meridians. In order to characterize the size of eye movements by one parameter this distribution is replaced by a circular distribution of equal area (see also Steinman, 1965) with a standard deviation σ . A moderately good estimate of σ is obtained by putting:

$$\sigma = \sqrt{\sigma_h \cdot \sigma_v}$$

This σ value is shown as a function of square size for the three subjects in figure 1.9.

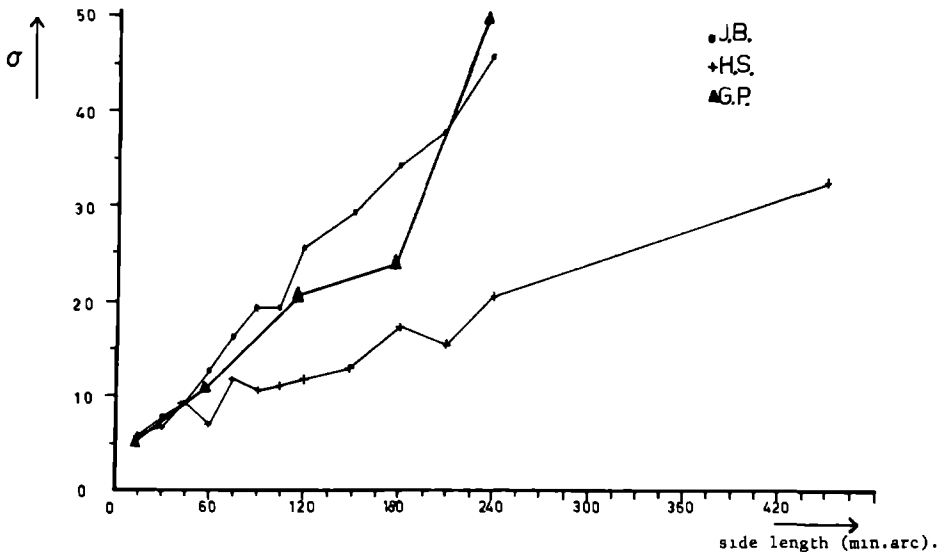


Fig. 1.9 Standard deviation σ (min.arc) as a function of length of the side of the observed square for the three subjects.

For all three subjects σ increases roughly linearly with the length of the side of the observed square.

For subject G.P. the value of σ obtained during the observation of the square with a side length of 240 min.arc exceeded the expectation. Some difficulties in maintaining the instruction with large targets were reported by subject G.P. The differences between the subjects might be attributed to intersubject variation such as training differences. Possibly there is also a difference in the interpretation of the instruction given. Whether these differences are essential for the maintenance of normal perception has been further investigated by using the recorded eye movements to move the same image under stabilized conditions (chapter 3).

1.4.3 The drift durations and the saccade rate

The change of the drift duration with square size is markedly different among the subjects. The mean drift duration decreases over the full range of square sizes for subject H.S. by about a factor 3, for subject G.P. by about a factor 1.5, for subject J.B. the mean drift duration stays about constant. The average saccade rate is for small squares about equal for the three subjects, viz. $0.8 - 1.2 \text{ s}^{-1}$. For large square sizes the average saccade rates are about 2.5, 1.9 and 1.3 s^{-1} for the three subjects H.S., G.P. and J.B., respectively. For the subjects H.S. and G.P. the standard deviation of the mean drift duration decreases more strongly than the mean value, which means that the occurrences of the saccades becomes more regular.

1.4.4 The saccade vector magnitude

The mean saccade vector magnitude increases with square size for all subjects. Figure 1.10 illustrates the increase of the mean saccade size as a function of square size for the three subjects.

Subjects J.B. and G.P. show an increase by about a factor of 5 in the mean saccade magnitude as the size of the square increases from 15 min.arc to 240 min.arc. Over the same range of square sizes subject H.S. shows an increase by about a factor of 3. Subject H.S. shows an additional increase during the

observation of the 450 min.arc square. For all subjects the standard deviation of the mean saccade magnitude is always about equal to half the mean saccade magnitude. The histograms obtained from horizontal and vertical saccade magnitudes show approximately normal distributions. When the creation of the two-dimensional plots of eye movements as shown in figure 1.8 was examined, it appeared that the saccades change the positions of the visual axis over the image according to approximately a bivariate normal distribution.

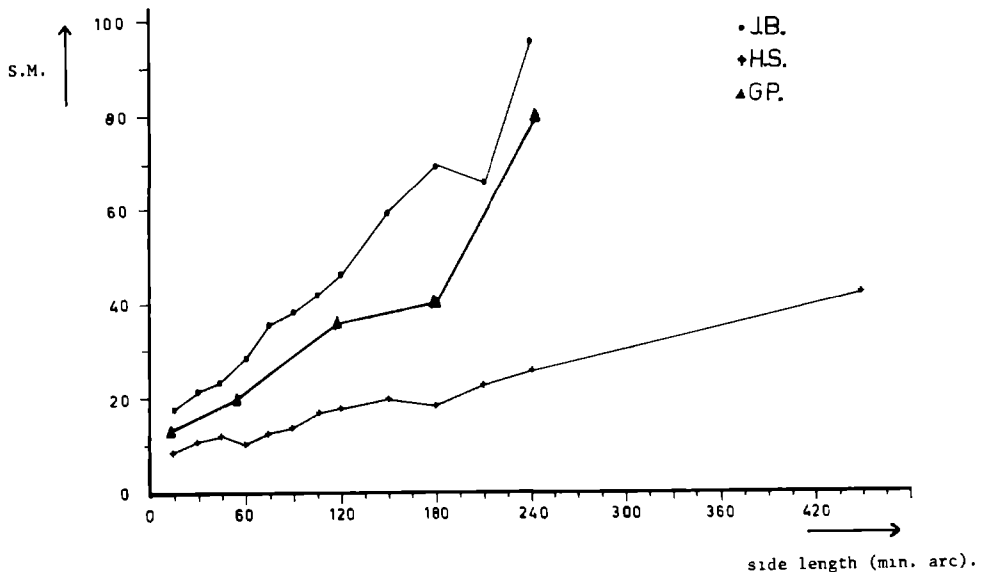


Fig. 1.10 The mean saccade vector magnitude S.M. (min.arc) as a function of side length of the observed square for the three subjects.

1.4.5 The mean drift vector magnitude and velocity

The mean drift vector magnitude of subject J.B. increases by about a factor of 1.7, of subject G.P. by about a factor 1.3 while subject H.S. shows no systematic change with square size. This drift vector magnitude is the size of the displacement of

the visual axis during an intersaccadic interval.

If one divides the drift vector magnitude by the drift duration one will get the drift vector magnitude per unit of time, i.e. a kind of average drift vector velocity. The mean of this quantity increases for all three subjects, viz. for J.B., G.P. and H.S. by a factor of 1.8, 2.0 and 3.2 respectively. The fact that the mean drift vector magnitude of subject H.S. does not depend on square size is the result of an increase in that average drift vector velocity and an equally large decrease of drift duration.

For the calculation of the mean drift vector velocity samples at 0.1 second time intervals were compared. These calculated velocities increase with square size roughly by the same factor for the three subjects.

The strategies followed by the three subjects in order to produce the greater eye mobility required during the observation of larger stimuli were somewhat different.

Subject J.B. produced larger saccades and drifts, with no systematic influence on the saccade rate.

Subject H.S. practically only produced larger and more frequent saccades, with no systematic influence on the drift vector magnitude. Subject G.P. mainly produced larger and more frequent saccades, whereas his drift vector magnitude slightly increased during the observation of larger stimuli.

For all three subjects the mean drift vector velocity increased about equally during the observation of larger stimuli.

1.4.6 The influence of the brightness of a square with sides of 4 degrees on the recorded eye movements

During preliminary experiments in which the subjects H.G. and H.S. were training for the given instructions we photographically measured the size of the pupil for the different brightness levels. Correcting for the Stiles-Crawford effect, the mirror used in the set-up and the glasses (used by H.S.) we calculated the effective retinal illumination level.

Table IV shows the effective retinal illumination levels for the two subjects under different stimulus conditions.

Table IV. Effective retinal illumination levels (effective trolands) for the two subjects under the different stimulus conditions.

Stimulus brightness		150 cd/m ²	27 cd/m ²	5 cd/m ²
$t_{d_{eff}}$	subject H.G.	2060	430	90
$t_{d_{eff}}$	subject H.S.	1670	290	70

Subject H.G. reported the utmost difficulty in maintaining a perception according to the I1-instruction (page 26). He reported regularly large changes in the perception of brightness in the centre of the square during this instruction. For that reason the eye movements of subject H.G., recorded during the I1-instruction which were in general smaller than his eye movements recorded during the I2-instruction, are not discussed any further.

Subject H.S. found himself well capable to follow both instructions. Figure 1.11 shows about 18 seconds of horizontal and vertical components of eye movements recorded during the observation of the square for the different brightness levels and instructions, subject H.S. Subject H.G. produced similar eye movements with smaller amplitudes.

The analysed properties of the recorded eye movements are given in table V.

For subject H.S. the influence of the used instruction on the produced eye movements is quite clear. The I2-instruction is accompanied by relatively larger and more frequent saccades in regard to the I1-instruction.

The influence of the brightness of the stimulus on the size of the mean drift vector magnitude is small for both subjects. A major influence can be observed in the occurrence of a smaller mean saccade vector magnitude with increasing brightness of the stimulus, whereas a slight increase in the mean saccade frequency occurs.

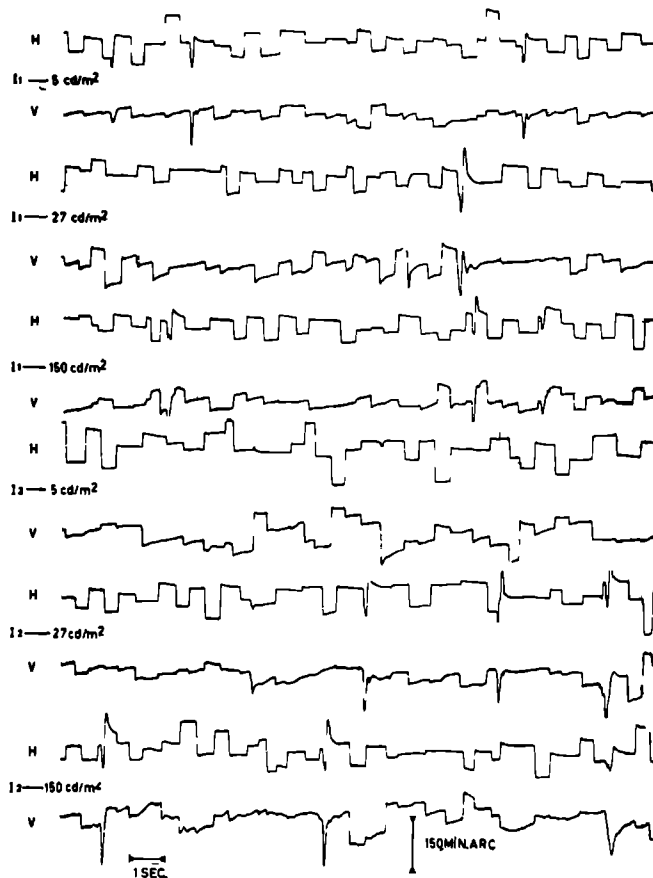


Fig. 1.11 Eye movements recorded during the observation of a square with sides of 4 degrees with different stimulus brightnesses and for the two different instructions indicated in the figure. Subject H.S.

Table IV. Analysed properties of eye movements while observing a square with sides of 4 degrees as a function of the brightness level and the used instruction.

	subject H.S. I1-instruction			subject H.S. I2-instruction			subject H.G. I2-instruction		
	5	27	150	5	27	150	5	27	150
stimulus brightness (cd/m^2)									
σ (min.arc)	21.5	22.1	18.6	38.2	32.8	31.7	25.1	31.5	17.9
mean drift vector velocity (min.arc/s)	24.0	29.0	23.4	29.2	35.5	40.1	20.8	28.5	25.5
mean drift vector magnitude and its standard deviation' (min.arc)	10.1	10.5	12.8	11.0	10.6	10.8	4.6	5.8	5.4
	6.7	7.1	8.9	7.7	9.3	8.5	3.0	5.3	3.5
mean saccade vector magnitude and its standard deviation (min.arc)	49.2	45.0	34.4	77.1	62.9	49.1	46.5	39.0	29.5
	29.3	21.8	21.3	43.8	34.7	38.2	25.6	26.4	18.8
mean intersaccadic duration and its standard deviation (s)	0.56	0.48	0.64	0.48	0.39	0.33	0.31	0.24	0.24
	0.37	0.24	0.41	0.31	0.24	0.17	0.12	0.10	0.11
mean saccade frequency (s^{-1})	1.8	2.1	1.6	2.1	2.5	3.0	3.1	4.0	4.0

1.5 Discussion

A comparison of our results with those obtained by other experimenters is restricted to the few reports concerning the accuracy of fixation and the occurrence of saccades as a function of target size.

Ditchburn and Ginsborg (1953) compared the eye movements made while fixating a small target to those made during the observation of larger fields of view.

Steinman (1965) reported on the accuracy of fixation as a function of target size, luminance and colour. In his experiments the size of the eye movements increased with the size of the target (target size: 1.9 - 87.2 min.arc), which is in accordance with our results. Steinman found that the saccade rate diminished with target size, while in our experiments the saccade rate increased with the target size for 2 out of 3 subjects (H.S. and G.P.). The other subject (J.B.) showed an approximately constant saccade rate.

Steinman also reported a reduction of the standard deviation of eye position with increasing luminance of the target. In accordance with his results we found a reduced standard deviation (σ) with the highest stimulus brightness. This was accompanied with a relatively smaller mean saccade vector magnitude. Sansbury et al. (1973) recorded eye movements of subjects attempting to maintain fixation during the observation of eccentric targets positioned 5 to 15 degrees off the fovea. They found that both the mean intersaccadic drift magnitude and the mean saccade vector magnitude increased with the eccentricity of the targets. The saccade rate was not influenced markedly or systematically.

In accordance with Sansbury et al. all three subjects in our experiments show an increase in the mean saccade vector magnitude with square size. Two of the subjects (J.B. and G.P.) show also an increase in the mean intersaccadic drift magnitude. The third subject (H.S.) has an approximately constant value of this quantity, but this is related to the decrease in mean drift duration (see section 1.4.5).

The main difference between our experiments and those

mentioned above is that we instructed the subjects to find and keep the minimal eye movements needed to maintain a satisfactory percept. In our experiments on the influence of target size the criterion for this percept was a homogeneously bright square with occasionally on and off borders. In our second series of experiments with subject H.S. the influences of the instruction on the recorded eye movements are shown. A more "normal" percept according to instruction I2 was accompanied by larger eye movements.

The intersubject differences found in the recorded eye movements are well known in studies on eye movements. Probably eye movements depend to a marked degree on the strategy, possibly influenced by the level of training and the sensitivity of the subject. Furthermore, the individually different criterion for the instructed perception adopted by the subject may have partly caused the differences in the eye movements in our experiments. In all cases the recorded eye movements were obtained from subjects who felt that they satisfied the criterion for an adequate continuous percept of the targets.

For small targets Steinman et al. (1967) showed the adequacy of drifts only for the maintenance of perception. When our subjects suppressed the saccades for periods up to about 20 seconds while fixating a small target (15 min.arc side) a loss of peripheral perception was reported (Troxler's effect). The foveal target was, however, normally perceived. These results reinforce the evidence that the small saccades in fixational eye movements (often called microsaccades) are not needed for normal foveal perception: drifts alone can ensure a normal foveal percept. On the other hand, these drifts during fixation are evidently inadequate to maintain the normal perception of large sized fields. For example when subject H.S. likewise suppressed saccades while fixating the surmised centre of a square of 4 degrees side he regularly reported the complete fading of perception, indicating that under these conditions his remaining drifts were in fact too small to ensure a normal percept.

It is obvious that greater eye mobility is needed to maintain the normal perception of larger squares. This greater

mobility is mainly brought about by the saccades.

The consecutive saccades have the effect of continually presenting parts of the square to new locations of the retina. The strong on-activities generated in these newly illuminated retinal areas evoke strong brightness activities which are, for the larger part, the sources which fill in, homogenise the whole square.

The gradual increase in effectiveness from small amplitude drifts to larger amplitude saccades with increasing eccentricity of the contours follows the well-known increase of the perceptive and receptive field diameter of the cells mediating the final percept.

To summarize, we conclude that the drifts are sufficient for small targets observed with the fovea and that the saccades are indispensable for large targets.

We used the constituent parts of the eye movements being recorded and analyzed to move a stabilized square of 4 degrees side. The efficiency of these parts for the preservation of the percept was thus also investigated.

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THE CORRELATION BETWEEN THE SACCADDES AND THE DRIFTS OF THE TWO EYES IN BINOCULAR FIXATIONAL EYE MOVEMENTS

2.1 Introduction

Ditchburn and Ginsborg (1953) measured the horizontal and vertical components of the movements of the two eyes during binocular fixation. However, only two of these four signals could be recorded at the same time. In general, they found that the results obtained under binocular and monocular viewing conditions differed little. They reported that small saccades occurred simultaneously in both eyes and that they were almost equal in magnitude and direction. The intersaccadic drifts were reported to be of two kinds: the vertical components were conjugate, both eyes moving upwards or downwards together whereas the horizontal components showed, in addition to conjugate movements, convergent and divergent movements which were approximately symmetrical for both eyes. From their results one might conclude that the saccades and also the vertical drifts in the two eyes are strongly correlated, while the horizontal drifts will probably show a weaker correlation because of the vergence movements.

Yarbus (1967) also reported a strong correlation of the saccades in binocular fixational eye movements. From visual inspection of the horizontal components of binocular fixational eye movements, the horizontal drifts were reported to be independent.

Krauskopf et al. (1960) also measured the horizontal components of binocular fixational eye movements and reported an overall correlation of the horizontal components of eye movements due to the simultaneous saccades, while drifts and tremor in the two eyes seemed to be uncorrelated. The evidence that drifts and tremor were not correlated was obtained from correlation of the drift and tremor positions of both eyes at widely spaced time intervals, viz. 2 seconds.

It appears that the results of these studies are conflicting as regards the correlation of the horizontal drifts in the two

eyes and that a good quantitative analysis of these movements up to now has not been made.

In order to study the role of eye movements in maintaining visual perception we developed methods for accurately measuring and analysing eye movements (see chapter 1). These methods are used to study the correlation between the movements of the eyes during fixation. The results obtained when both eyes were fitted with silicone eye coils show that the saccades and the vertical drift components are strongly correlated in the two eyes. The horizontal drift components in both eyes showed a weaker correlation, which probably is caused by the time varying vergence. In general our results are in agreement with the qualitative description of binocular fixational eye movements as given by Ditchburn and Ginsborg (1953).

In our experiments we also used a modified suction cap for measuring eye movements. As a general rule, the suction cap follows eye movements correctly, which is proved by the experiments with stabilized images (Gerrits et al. 1966; 1970; chapter 1). Some of our subjects preferred to use the suction cap for measuring eye movements, and in general it is easier to handle than a silicone eye coil. However, the suction cap is larger and heavier than a silicone eye coil and as we were interested in knowing whether the suction cap hampers the eye movements, we compared the eye movements measured with the suction cap and with the silicone eye coil. From experiments in which one eye was fitted with a suction cap device and the other eye with a silicone eye coil, it was found that the suction cap reduced the eye movements by about 20 percent. This reduced eye mobility is caused by the frictional and viscoelastic forces applied to the cap by the eyelids.

2.2 Methods

The horizontal and vertical components of the eye movements were recorded using a magnetic-field, search-coil technique (chapter 1).

In order to measure binocular eye movements, both eyes were fitted with search coils. The voltages induced during eye movements

in the two search coils were recorded by two pairs of lock-in amplifiers (Princeton Applied Research, model 128 A). During the measurements the subject was supine with his head placed in the magnetic field cube. Before each session the subject's head was positioned accurately, placing the two eye coils on the central axis of the horizontal pair of field coils, in such a way that the distances of the two eye coils to the centre of the magnetic field cube were equal, which ensured equal field strength at the positions of both eye coils. The head was fixed in that particular position with the aid of a suction pillow. As the search coils used were always identical an equal sensitivity for the binocular measurements of fixational eye movements was guaranteed. For eye movements smaller than about 1 degree the linearity of the measurement system under these conditions is better than 99 per cent.

During the experiments, which lasted each about 4 minutes, subject H.S. binocularly fixated a white square with a side of 15 min.arc, produced on a television screen. The brightness of the square was always 150 cd/m^2 , while the background was about 3 cd/m^2 . The distance from the subject's eyes to the screen measured 182 cm.

2.2.1 The eye attachments

Both eyes were fitted with a silicone eye coil for measuring binocular fixational eye movements (Collewijn, 1975). Like Collewijn, we did not find any evidence for silicone eye coil slippage on the eye or any influence on the characteristics of the eye movements. When using these silicone eye coils, the eyes were anaesthetised with Novesine (0.2 per cent). Because of the anaesthesia the blink reflex was not as active as normal, which could easily result in drying-out of the cornea, causing poor vision. In order to prevent this drying-out, the subject was asked to blink regularly which ensured that good vision was maintained. The visual acuity of the subject was regularly checked before and after each recording.

In the experiments in which the influence of the suction cap device on the recorded eye movements was investigated (see introduction), the subject's right eye was fitted with a suction cap

device and the left eye with a silicone eye coil. For the measurements of eye movements the suction cap was modified with a holder for a search coil and fitted with flat glass to give normal vision (see chapter 1). The mass of the suction cap including the search coil measured 1.8×10^{-3} kg while the silicone eye coil weighed only 0.1×10^{-3} kg.

2.2.2 The analysis of binocular fixational eye movements

The measured eye movements were recorded on a 12 bit pulse-code modulated recording system (Kaiser, Munich). Four channels were recorded simultaneously at a rate of 500 samples per second for each channel. The recorded eye movements were analysed with the aid of a digital computer. Samples were taken at a rate of 400 for each channel with an accuracy of 12 bits and stored on disk.

The overall system bandwidth was 180 Hz (-3 dB), the peak to peak noise level was about 20 sec.arc. Up to 180 consecutive seconds of binocular horizontal and vertical components of eye movements could be stored in one file on disk.

The moments of on- and offset of the saccades and blink-associated eye movements were determined separately for each eye to enable the saccadic and intersaccadic components of eye movements to be analysed (see also chapter 1).

From the recorded eye movements we calculated separately for each eye:

1. The standard deviations of the horizontal and vertical components of eye movements, σ_h and σ_v respectively.
2. The mean duration of the intersaccadic intervals (drift duration) and standard deviation.
3. The mean vectorial saccade magnitude and standard deviation.
4. The mean vectorial drift magnitude and standard deviation, the drift magnitude being defined as the difference between the positions at the moment of offset of a saccade and the moment of onset of the next saccade.
5. The vectorial drift velocity computed from drifts digitized at 0.1 second time intervals in the intersaccadic periods.

In addition we calculated the mean value and standard deviation of the distribution of correlation coefficients (Pearson r 's) obtained from successive parts in the records of the horizontal and vertical components of binocular eye movements. Up to a maximum of 1024 samples of horizontal and vertical eye movements at a 2.5 millisecond time interval (corresponding to maximal 2.56 seconds) could be correlated each time. Always a large number (about 60) of correlation coefficients obtained from successive parts in the records were used to calculate the mean value and the standard deviation.

2.3 Results

2.3.1 Binocular fixational eye movements measured with silicone eye coils

About 11 seconds of binocularly recorded horizontal and vertical components of eye movements with the horizontal and vertical discrepancy signals are shown in fig.2.1 The horizontal and vertical discrepancies represent the differences between the horizontal and vertical components of eye movements respectively.

As may be seen from the records of the simultaneous horizontal and vertical components, the saccades were strongly correlated in the two eyes. The correlation of the saccades and the correlation of the vertical intersaccadic drift movements were quite clear. The horizontal drifts show a weaker correlation, probably because of small vergence movements.

The discrepancies are due to differences in the magnitudes of both the saccades and the drifts. The horizontal discrepancy is distinctly larger than the vertical discrepancy. This is caused by the fact that the difference in the horizontal drifts is markedly larger than the vertical drift difference. Usually the contribution of the saccade differences for the horizontal direction is even smaller than for the vertical direction.

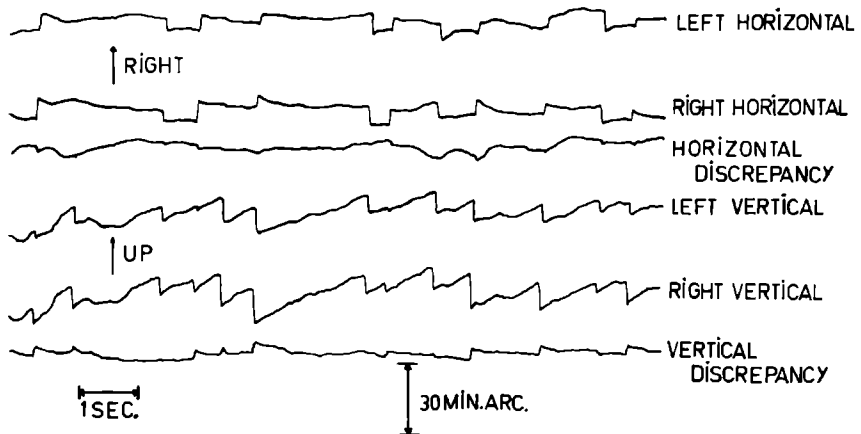


Fig.2.1 Binocular fixational eye movements with the horizontal and vertical discrepancy signals, measured with silicone eye coils on both eyes.

Quantitative data obtained from a representative record of 180 seconds of binocularly recorded fixational eye movements, measured with silicone eye coils on both eyes, are given in table I.

These data show that the right eye produces larger eye movements than the left eye. Both the mean saccade and drift magnitudes were about 13 per cent larger than in the left eye. The eye movements during binocular fixation for this subject were about two times larger than during monocular fixation of the same target (see chapter 1). This was caused by the occurrences of larger saccades; the drifts under binocular and monocular viewing conditions were found to be somewhat smaller. Also, the frequency of the saccades was about two times higher than during monocular fixation of the same target (see chapter 1).

Table I. Analysed characteristics of binocular fixational eye movements; silicone eye coils on both eyes.

	σ_h σ_v (min.arc)	Mean drift duration (second)	Saccade vector magnitude (min.arc) mean \pm s.d.	Drift vector mag- nitude (min.arc) mean \pm s.d.	Drift vector velocity (min.arc/s)
Right eye	9.6 15.6	0.5 \pm 0.4	12.7 \pm 7.5	6.5 \pm 4.5	23.8
Left eye	7.8 12.4	0.5 \pm 0.4	11.1 \pm 5.9	5.8 \pm 5.0	22.3

The mean value and the standard deviation of the distribution of the correlation coefficients for the saccades and drifts and the drifts separately were calculated from a large number (about 60) of values of the correlation coefficients obtained from successive parts in the records. These values are given in table II.

Table II. Mean value and standard deviation of the distribution of the correlation coefficients of binocular fixational eye movements; silicone eye coils on both eyes.

	Saccades and drifts	only drifts
Horizontal	0.9 \pm 0.1	0.7 \pm 0.3
Vertical	0.9 \pm 0.1	0.8 \pm 0.2

In general the horizontal and vertical eye movements were strongly correlated due to the simultaneous saccades, which is in accordance with the results obtained by Krauskopf et al. (1960). The vertical drift movements also showed a strong correlation. The horizontal drift movements showed a strong positive correlation on most occasions, but in some intersaccadic periods following a blink-associated eye movement, no or even negative correlations were obtained. A blink could presumably cause a change of vergence which was corrected in the next intersaccadic movements. Negative correlations were not found for the vertical drift movements.

When we correlated the horizontal and vertical components of the eye movements measured at one particular eye no correlation at all was found. In normal eye movements the horizontal and vertical components are uncorrelated to each other.

In general the results obtained were in accordance with the qualitative description of binocular fixational eye movements given by Ditchburn and Ginsborg (1953).

2.3.2 Binocular fixational eye movements measured while the right eye was fitted with a suction cap device and the left eye with a silicone eye coil.

About 21 seconds of binocular fixational eye movements recorded with a suction cap device and a silicone eye coil are illustrated in fig. 2.2.

In accordance with Robinson (1963) and Ginsborg (1952) the blinks do not obey Bell's phenomenon. If Bell's phenomenon were obeyed one would expect upwards and outwards movements of the eyes, but during blinks both eyes moved downwards and nasalwards. When the eyelids closed voluntarily for a somewhat longer period after the usual first blink movement, a second movement according to Bell's phenomenon was observed; the eyes moved slowly upwards and outwards.

It is also remarkable that most of the horizontal saccades and some of the vertical saccades recorded with the suction cap device showed small overshoots, which normally had never been observed with this subject.

LEFT EYE: EYE COIL

RIGHT EYE: SUCTION CAP DEVICE

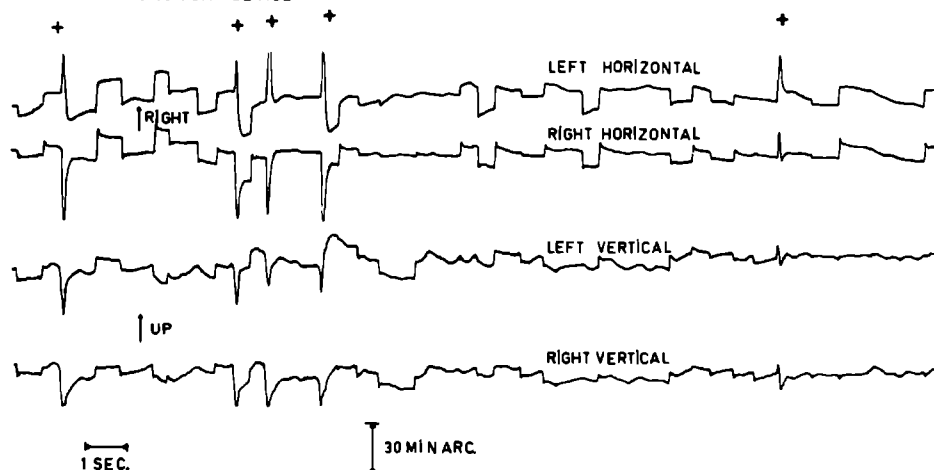


Fig. 2.2 Binocular fixational eye movements containing some blinks (indicated by crosses), measured with a silicone eye coil on the left eye and a suction cap device on the right eye.

Quantitative data obtained from a representative record of 180 seconds of binocular fixational eye movements measured with the aid of a suction cap on the right eye and a silicone eye coil on the left eye are given in table III.

Table III. Analysed characteristics of binocular fixational eye movements; a silicone eye coil on the left eye and a suction cap device on the right eye.

	σ_h σ_v (min.arc)	Mean drift duration (second)	Saccade vector magnitude (min.arc) mean \pm s.d.	Drift vector mag- nitude (min.arc) mean \pm s.d.	Drift vector velocity (min.arc/s)
Right eye	14.6 13.9	0.5 ± 0.4	15.2 ± 11.2	6.1 ± 6.2	24.9
Left eye	18.8 14.9	0.5 ± 0.4	19.6 ± 7.1	7.6 ± 7.1	29.9

In contrast with the previous experiment, the right eye showed smaller saccades and drifts under these conditions than the left eye. Also remarkable was the general increase in the size of the binocular fixational eye movements under these conditions which has not been understood.

It also emerged that in particular the horizontal drifts were limited by the suction cap device. In fig.2.3 this influence of the suction cap on the horizontal drift is clearly demonstrated, especially when the subject suppressed the saccades for a short period.

BINOCULAR FIXATIONAL EYE MOVEMENTS
LEFT EYE EYE COIL
RIGHT EYE. SUCTION CAP DEVICE

SUBJECT HS

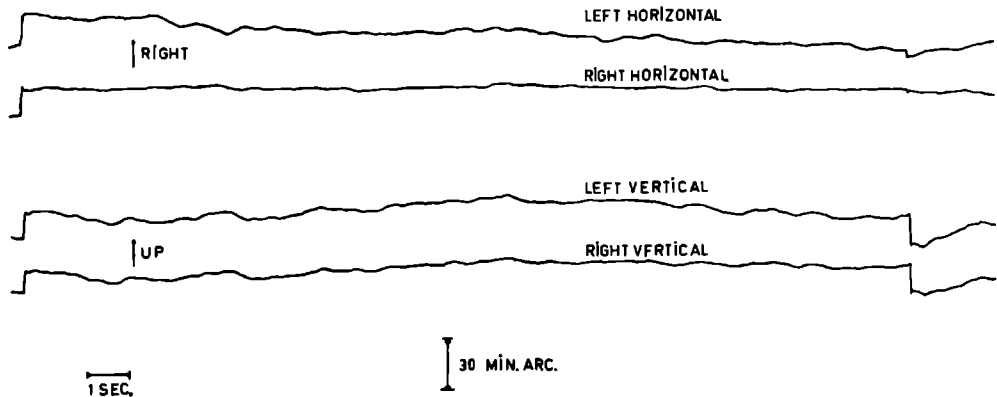


Fig.2.3 Binocular fixational eye movements measured with a silicone eye coil on the left eye and a suction cap device on the right eye, while the saccades were suppressed.

The mean value and the standard deviation of the distribution of the correlation coefficients for the saccades and drifts and the drifts separately were calculated from a large number (about 60) of values of the correlation coefficients obtained from successive parts in the records. These values are given in table IV.

Table IV. Mean value and standard deviation of the distribution of the correlation coefficients of binocular fixational eye movements; a silicone eye coil on the left eye and a suction cap device on the right eye.

	Saccades and drifts	only drifts
Horizontal	0.9 ± 0.1	0.3 ± 0.5
Vertical	0.9 ± 0.1	0.8 ± 0.2

Because the suction cap mainly limited the horizontal drift, the correlation for the horizontal drift components was markedly weaker than in the previous experiment (see table II).

The saccades and drifts measured with the suction cap were smaller than those measured with the silicone eye coil. Probably this is caused by viscoelastic and frictional forces exerted on the suction cap by the eyelids.

Experiments in which the eyelids were pulled from the suction cap device and the silicone eye coil showed a decrease in the drift movements measured with the silicone eye coil, while the drifts measured with the suction cap showed a small increase which can be attributed to the loss of frictional and viscoelastic forces on the suction cap applied by the eyelids.

The fact that the magnitude of the drifts measured under these conditions with the silicone eye coil actually decreased was not expected. An explanation for this might be that the pulling-apart of the eyelids causes a strain on the conjunctiva which reduces eye mobility.

2.4 Discussion

Besides confirming the established opinion that the saccades are correlated in both eyes (Yarbus, 1967; Krauskopf et al. 1960; St Cyr and Fender, 1969; Williams and Fender, 1977) our

experiments at the same time demonstrate the correlation of the drifts in the two eyes during binocular fixation. Our results are consistent with the qualitative description of binocular fixational eye movements as given by Ditchburn and Ginsborg (1953). The confusion in the literature about correlated saccades and uncorrelated drifts (Yarbus, 1967; Krauskopf et al., 1960), based on the analysis of the horizontal components of binocular eye movements, is understandable because of the general weaker correlation of the horizontal drifts in the two eyes. Vergence movements acting symmetrically in opposite horizontal directions on both eyes are the reason for this weaker correlation.

Steinman et al. (1967) showed that the saccades in fixational eye movements could be suppressed for 10 seconds or more by practised observers without any reduction in the accuracy of fixation. From these results it has been concluded that the remaining drifts are able to maintain eye positions steady and must therefore be under a central control; they cannot be attributed simply to system noise.

Also our results suggest that both the saccades and the drifts in both eyes are under a control common to both.

When both eyes were fitted with silicone eye coils, the right eye produced the largest eye movements. In contrast, the left eye, fitted with a suction cap device, produced smaller eye movements than the right eye. In particular the horizontal drift is hampered by the suction cap (see fig. 2.3). As is shown, frictional forces in the horizontal direction applied by the eyelids on the cap caused this effect. From this observation and the investigation of the influence of the eyelids, we concluded that a suction cap device changed the natural eye movements normally produced. In the normal situation, the silicone eye coil produced the largest eye movements, which suggests that frictional and viscoelastic forces applied on the silicone eye coil are very small. Because of its easy handling a suction cap in our opinion is still very attractive in experiments with small eye movements. The silicone eye coil is our most favourable eye attachment for the precise measurement of natural eye movements

although a comparative examination with an accurate measurement of binocular eye movements without any attachment to the eye is still needed.

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THE IMPORTANCE OF THE SACCADIC AND DRIFT MOVEMENTS FOR THE PERCEPTION OF A BRIGHT SQUARE IN PARAFOVEAL STABILIZED VISION

3.1 Introduction

In experiments with stabilized retinal images the perception disappears within a few seconds, the eye movements occurring in normal vision are responsible for the maintenance of the perception. Gerrits en Vendrik (1970a;1970b;1974) have shown that the perception of a faded stabilized image of a homogeneously illuminated field can be restored by appropriate movements of the contours only. The brightness generated by the movements of the contours was seen to spread far beyond the location over which the contours had been moved. This spread of brightness (or darkness), homogenizing the whole field, is called the 'filling-in'.

In their experiments Gerrits and Vendrik (1974) moved a bright square with sides of 4 degrees on a television screen with sinusoidal and triangular signals of adjustable amplitude and frequency. Besides these regular movement signals Gaussian and binary noise signals were used to imitate the drift and the microsaccadic movements of the eye respectively. The subject observed these stimuli through a flexible optic fiber which was fastened to the suction cap used to obtain stabilization. From their results these authors concluded that the most effective eye movement preserving vision is better characterized by its quality (irregularity and continuity) than by its name (drift or saccade).

The choice of the amplitude and frequency components of the noise signals they used to imitate the drifts and the microsaccades of the eye movements was determined by the scanty data available in the literature at that time.

They concluded that real eye movements had to be recorded in order to investigate the importance of the saccades and the drifts for the perception of brightness and contours in normal vision.

For this reason we measured and analysed the eye movements of 2 subjects (H.S. and H.G.) looking at a bright square with sides of 4 degrees under different instructions and retinal illumination levels (see chapter 1, section 1.4.6). During these experiments the subjects were asked to look in the direction of the surmised centre of the square and to minimize their eye movements as much as possible while still preserving vision of the square according to the criterion.

These eye movement signals have been used to move a bright square with the same set-up as used by Gerrits en Vendrik (1974). In this chapter we describe the difficulties encountered and the results obtained when the stimulus (a bright square with sides of 4 degrees) was moved with:

- a. previously recorded eye movements (section 3.3)
- b. selected parts of previously recorded eye movements, i.e. those parts which contained no blinks (section 3.4)
- c. artificially generated eye movements, i.e. signals imitating accurately the saccades and the drifts in the eye movement records (section 3.5)
- d. artificially generated eye movements as used formerly by Gerrits and Vendrik (1974) (section 3.6).

In the first series of experiments the retinal illumination level of the stimulus amounted to about 40 effective trolands, which was markedly lower than the retinal illumination level during the measurements of eye movements (see chapter 1, section 1.4.6 table IV). In later experiments we had the opportunity to increase the amount of light reaching the retina by modifying the suction cap and the adjustment of the used television monitor. This enabled us to investigate also the influence of the retinal illumination level on the quality of the perception generated by the stimulus movements.

3.2 General method

The method described by Gerrits and Vendrik (1974) was used to study the perception of a stimulus which was moved over

the retina under stabilized conditions. A television screen is imaged on one end of a viewing fibre. The other end, made very flexible by removing the cover, is attached to a stabilization cap sucked to the eye. The field of vision measured 13 degrees in dia. In our first series of experiments the brightness of the stimulus generated on the television screen measured 150 cd/m^2 , while the background brightness measured 3 cd/m^2 . The retinal illumination level measured about 40 effective trolands in these conditions as a result of losses in the fibre, lenses and the artificial pupil ($\emptyset = 2 \text{ mm}$). The amount of light reaching the retina was adjustable by modifying the adjustment of the television monitor and the diameter of the artificial pupil in the suction cap. The diameter of the individual fibers measures $10 \mu\text{m}$, corresponding to a viewing angle of 1.8 min. arc . in the used set-up (50 D lens in the suction cap). At contours passing through the fovea the individual fibers can be observed. Therefore the contours of the used stimulus were located outside the foveal area where the individual fibers were no longer observable. In our experiments the stimulus was a homogeneously illuminated square with sides of 4 degrees. The centre of the stimulus was projected in the middle of the fovea. When the stimulus is moved on the television screen the image moves over the retina. Besides the brightness perception elicited by these stimulus movements the subjects also observed these movements. In our experiments the subjects were instructed to pay no attention to the perceived movements. Only the quality of the perception of the stimulus was evaluated (see below).

During these experiments a thin black stalk ending in a small disk (diameter 20 min. arc .) was situated in front of the moving square against the television screen. This stationary black disk was projected on the fovea. Because the stalk and disk were immobile with respect to the subject's retina they normally disappeared from vision. Their occasional reappearance indicated to the subject that he made too large eye movements causing a shift of the suction cap and thereby of the stimulus with respect to the retina. In all experiments the subject's eye was anaesthetised with Novesine (0.2 per cent), while the non

stimulated eye was covered with a black cloth.

Preliminary psychophysical experiments were carried out in order to characterize the various stages of perception obtained with increasing stimulus movement amplitudes. Gerrits and Vendrik (1974) in their study on the influence of stimulus movement on the perception of a stabilized homogeneously illuminated square with sides of 4 degrees described a number of distinguishable perceptions occurring with increasing effectiveness of the stimulus movement amplitudes. In preliminary experiments the various stages were studied by two trained subjects (H.S. and H.G.) taking part in all experiments. They described their percepts verbally and by means of drawings. Although differences in the effectiveness of the various stimulus movement amplitudes among the two subjects were observed, these preliminary experiments resulted in various stages of perception to be used as criteria in the experiments. A scale numbering from 0 to 10 was adopted. Six stages were distinguished assigned by the even numbers of the scale, meaning:

- 0- Nothing at all, or only occasionally on and off borders while the rest of the stimulus remained as dark as the background.
- 2- A square with on and off borders and a very weak brightness in the centre which is just detectable more than the background.
- 4- A square with on and off borders and a weak brightness in the centre which is clearly more than the background.
- 6- A square with on and occasionally off borders and a centre brightness which is clearly lower than the on borders.
- 8- A homogeneously bright square with occasionally on borders near the contours.
- 10- A homogeneously bright square without any borders near the contours.

In addition to the even numbers of the scale sometimes also the uneven numbers of the scale were adopted by our subjects for a percept value in between the above described stages. Starting from a completely faded image both subjects needed about 20 to 30 seconds of observation before the midpart of the moving square had acquired its maximal brightness level which,

however, still fluctuated in the course of time. They needed 2 - 3 minutes of observation before they could decide on the quality of the perception (0-10). The subjects needed this time to average the fluctuating percept and to discard those parts of the observation in which percepts were generated by destabilization.

In each session, lasting about 1 hour, 15 different movement signals could be presented.

3.3 Previously recorded eye movement signals: method and results

It seemed rational to move the stabilized $4^{\circ} \times 4^{\circ}$ bright square with the original eye movements recorded when the subject observed this square according to the instruction given in the non-stabilized condition. In this way the role of the eye movements could be evaluated by the percepts generated. The retinal illumination of the stimulus amounted to about 40 effective trolands. In total 5 sessions have been spent for this investigation.

When subject H.S. used his previously recorded eye movements during the observation of a square with sides of 4 degrees (see chapter 1; table III), the quality of the obtained perception was evaluated with about 6, which to his opinion was quite well in accordance with the quality of the perception as occurring during the measurement of these movements. However, it was seen that besides the saccades and drifts the original eye movements contained large blink associated eye movements, normally occurring 3 to 7 times per minute, which may have contributed to this percept in some periods. These movements easily spoil the investigation of the efficiencies of the saccades and drifts in generating a perception. Especially when small amplitude eye movements were studied which just generated a weak perception these blink associated eye movements were very disturbing in stabilized condition because they sometimes caused the bright square to move partly outside the field of vision temporarily. In normal vision these large momentary displacements of the stimulus do not disturb the perception.

For subject H.G. previously recorded eye movements have been used as described in chapter 1, table V (150 cd/m^2).

Also subject H.G. found these blinks extremely disturbing and he was not able to attribute a reliable value to his perception under these conditions.

From these experiments we concluded that in order to investigate the importances of the saccades and the drifts, blink free movements were needed which should last about 2 to 3 minutes in order to be evaluated by the subjects. However, it was found previously (chapter 1) that the quality of the image deteriorated very soon when the subject refrained from blinking; moreover this was painful. Therefore we decided to use parts of the eye movements containing no blinks.

3.4 Repeatedly presented eye movement signals: method and results

In order to obtain suitable eye movement records for the selection of blink-free parts we recorded eye movements again, now using different instructions during the observation of the bright square with sides of 4 degrees. The brightness of the square measured 150 cd/m^2 , the background 3 cd/m^2 . H.S. and H.G. participated again as subjects. Part of the record containing no blinks was selected and presented repeatedly by a PDP 11/45 computer ("endless loop"). The length of this part was about 8 seconds.

The eye movements elicited by looking at the centre of the bright square and fulfilling the criterion for a percept of a reasonably bright square with on and off borders near the contours (according to about qualification value 6) have been called "restrained eye movements".

The eye movements made when the subject was ordered to move the fovea freely, but within the square and thereby giving rise to a very good quality of perception (according to about qualification 8 to 10) have been called "forced eye movements".

The eye movements made when the subject tried to suppress them, during which he succeeded regularly to get rid of the saccades for periods of time up to about 10 seconds, have been called "suppressed eye movements". During these trials alternatively no perception at all and a very weak perception (perception value about 4) was observed. In the following experiments (8 sessions) a similar bright square with sides of 4 degrees,

stabilized on the subject's retina, was set in motion with repeatedly presented parts of these recorded movements. From the experiments carried out it is concluded that both subjects obtained a good quality of perception with the repeatedly presented parts of the "forced eye movements". The perceptions were evaluated around 8. The repeatedly presented parts of the "restrained eye movements" were evaluated around 5. The repeatedly presented parts of the "suppressed eye movements" still contained some small saccades besides the remaining drift movements. The prevailing periods of drifts were found to result in a complete fading of the perception (evaluated 0) within a short time. Other parts containing some small saccades restored the perception up to a value of maximally 4. In general both subjects observed more brightness when the stimulus was displaced over larger amplitudes. The percepts particularly those generated with the movements obtained under the former restrained and suppressed instructions, fluctuated heavily. According to the subjects these fluctuations were strongly correlated with the movement patterns. In fact our subjects succeeded in recognizing the movement patterns, reappearing once in about 8 seconds. So a particular part of the recordings generating less brightness, because of a diminished movement present momentarily, was observed again and again. The parts without blinks in the eye movement recorded from our subjects and used to generate the "endless loop" were obvious too short.

The percepts generated did not quite meet the evaluation values obtained during the recording of the eye movements. One of the reasons may be that the fluctuation in the eye movements causes fluctuations in perception which are better seen in stabilized condition than in normal vision. Another cause may be that the retinal illumination level during the recording measured about 1670 effective trolands (H.S.) and 2050 effective trolands (H.G.) while in stabilized condition the retinal illumination level amounted to only about 40 effective trolands for both subjects.

3.5 Artificially generated eye movements

As we did not succeed to use the original eye movement

signals to investigate the role of the saccades and drifts separately and together, we decided to use artificially generated movement signals imitating the properties of the saccades and the drifts for this purpose.

A great advantage of these artificial movements is that they easily can be duplicated and used by anybody who wants to investigate the influence of eye movements on perception or cell responses, or more strictly speaking the influence of similar movements with respect to the retina. These artificial movements can be adapted to the mean properties of the drifts and saccades as occurring in different subjects and situations. Moreover the amplitudes and frequencies of the artificial movement signals can be varied in order to investigate the results obtained by an extended range of drift or saccade magnitudes.

The possibilities mentioned above have been practised in the experiments described below. In addition the influence of the retinal illumination level on the percepts elicited by these artificial eye movements has been investigated. In total 64 successful sessions have been spent in this investigation. Soon after the start of these experiments differences between the observations reported by subject H.S. and H.G. manifested themselves. These differences are partly due to difference in training in visual observation, and the ability to observe brightness differences in a field. On the other hand they may also reflect a different intrinsic effectiveness of drift and saccadic movements for the subjects as also differences had been found in the eye movement records (chapter 1, table V). Subject H.G. found himself unable to fit his observations completely in the scale adopted before (section 3.2).

Therefore a row of drawings has been produced (numbered correspondingly to the scale values from 0 - 10).

Drawing 10 represented a homogeneous bright square of 100% brightness; in drawings 8, 6, 4 and 2 the centre brightness was substituted by 87, 75, 60 and 30% of the centre brightness of drawing 10 respectively. Additionally in drawings 8, 6, 4 and 2 on borders were indicated.

Before each experiment the subjects refreshed their memory by

consulting these drawings. For subject H.S. these drawings were not helpful because he was unable to memorize these drawings as references during the experiments. Therefore subject H.S. persisted in using the scale adopted. He mainly estimated the centre brightness with regard to the brightness level of the on borders to evaluate the percept. Subject H.G. found these drawings quite helpful and refreshed his memory consulting these drawings before and eventually during the sessions. The scale number attributed to a certain observation depended not only on the ratio of centre brightness and the brightness of the on border but also on the absolute brightness level. E.g. a small to and fro movement resulting in a completely homogeneous square did not deserve a scale number 10 for that moment if, according to the subject's judgement, the brightness was too low (lower than the non-stabilized square).

Subject H.G. described his observations extensively (recorded on tape) because still a number of observations was made not fitting any list (e.g. the centre of a square partly bright-partly dark; only brightness in a triangular or rectangular part of the square, etc.).

Finally it should be remarked that subject H.G. evaluated a percept with 8 even when the on borders were observed continuously.

3.5.1 The artificial drift movements: acquisition and use

With the aid of a PDP 11/45 computer we calculated the amplitude spectrum for the drifts present in the eye movements as function of square size (chapter 1).

The results obtained for the different subjects showed that the amplitude spectrum decreases with approximately 6 dB/octave till about 3 Hz and with approximately 12 dB/octave above 3 Hz, irrespective of square size.

Computer analysis confirmed that Gaussian noise with a bandwidth from 0 - 150 Hz, generated by a Hewlett and Packard Generator (HO-1-37222A) and filtered with a filter which was flat from 0 Hz up to 0.1 Hz and decreased with 6 dB/octave between 0.1 and 3 Hz and with 12 dB/octave above 3 Hz had approximately the same spectral properties as drifts.

In our experiments this filtered noise was used to imitate the drifts. The amplitudes could be adjusted in order to study a range of drift amplitudes extending the physiological values. Because we found no correlation between the horizontal and vertical components in normal eye movements (chapter 2, page 53), we used two uncorrelated artificially generated signals for the imitation of the horizontal and vertical drift components. These artificial signals were used in the experiments. A signal with a standard deviation of 6.3 min.arc is called the standard signal and its amplitude is signified with 1 AD (abbreviated from Artificial Drift). The mean vectorial drift velocity measured 21 min. arc/s. The peak to peak amplitude is estimated as six times the standard deviation, being 38 min.arc. An example of about 16 seconds of the artificially generated drift signals is illustrated in figure 3.1. In the experiments these signals were made smaller or magnified in order to study the efficiencies of a range of drift amplitudes for the generation of perception.

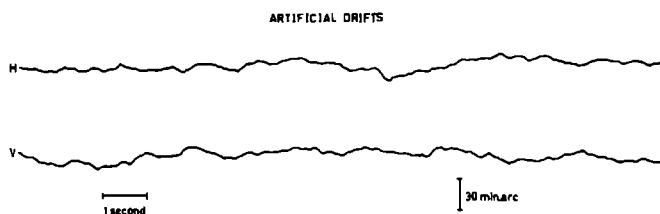


Fig.3.1 An example of the horizontal and vertical components of our artificially generated drifts. The amplitude is 1 AD (see text).

In figures 3.2 and 3.3 for subject H.S. and H.G. respectively the perception values illustrated are obtained from the experiments in which a centrally fixated bright square with sides of 4 degrees was moved over the retina by means of the artificially generated drift movements. The range of the perception values is indicated by the length of the line, while the

symbol indicates the modal value. In a few cases two symbols are indicated, meaning that both these perceptual values were obtained most often. The artificial drift amplitudes studied are 0.5 AD and 1 AD up to 8 AD in steps of 1 AD. The first series of experiments were performed with a stimulus with a retinal illumination level of about 40 td_{eff} for both subjects. In a second series of experiments the retinal illumination level was increased up to about 480 td_{eff} .

Subject H.S.:

Drift amplitudes of 1 AD and lower resulted in a range of perception value from 0 - 4. No influence of the retinal illumination level of the stimulus on the efficiency of the artificial drift movement is found (see figure 3.2).

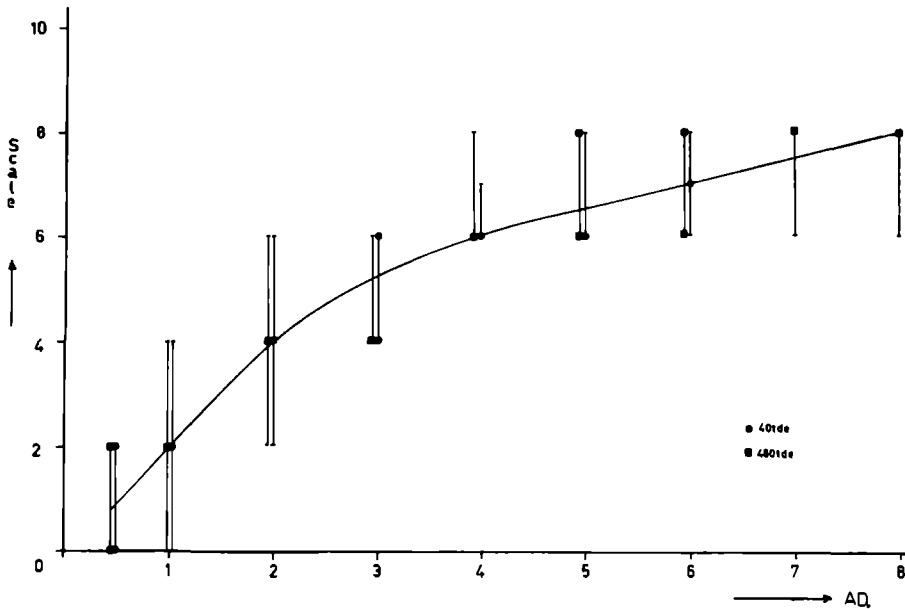


Fig.3.2 Perceptual value as function of the amplitude of the artificial drift movement and the retinal illumination level; subject H.S.

Subject H.G.:

The diagram in figure 3.3 indicates the results of two groups of measurements: results denoted with "older" measurements (connected by the curves) and "newer" experiments (indicated by dotted lines and cross symbols in the diagram). These newer results have been obtained in better controlled experimental conditions (image sharpness and condition of the subject's eye). In the newer experiments subject H.G. studied artificial drift amplitudes of 1.0 ; 1.3 ; 1.5 and 1.7 AD respectively.

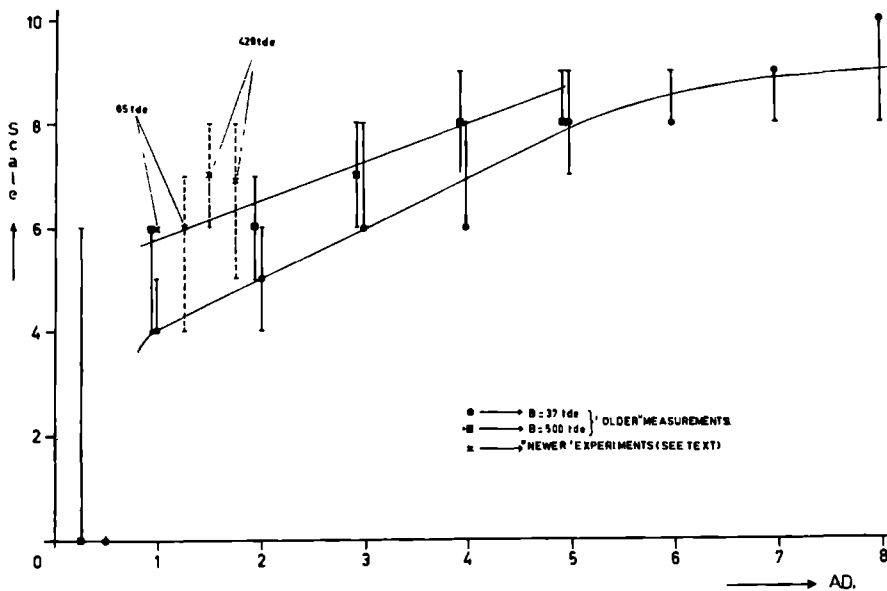


Fig. 3.3 Perceptual value as function of the amplitude of the artificial drift movement and the retinal illumination level ; subject H.G.

It is clear that the artificial drift movements are more effective for H.G. than for H.S.: the percept never becomes 0 for an amplitude of 1 AD.

According to the older measurements for the subject H.G. there

exists a marked influence of the retinal illumination level on the results, in the newer outcomes this influence is less clear.

3.5.2 The artificial saccadic movement: acquisition and use.

The analysis of eye movements showed that the saccades distributed the positions of the eye approximately to a bivariate normal distribution. Therefore we imitated the saccades by taking a signal having jumps with normally distributed amplitudes. Two signals, for the horizontal and vertical positions respectively, were generated by taking samples from two uncorrelated Gaussian noises with a bandwidth from 0 to 15 Hz generated by Hewlett and Packard Generators (HO-1-37222A). The two sample values are hold until a trigger signal was given, at which two new samples were taken and so on.

The differences in the positions before and after the trigger moment represented the saccadic displacement. By means of filtering the duration of the saccades was increased up to about 25 millisecond which is the normal value (Ditchburn 1973).

Normally the size of the eye movements is increased by an increase of the mean saccade size. Often also the mean saccade frequency is increased with increasing eye movements (see chapter 1).

For technical reasons we only used constant saccade frequencies. The possible influence of a variation of the saccade intervals has not been investigated in these experiments. However, with the increase of the mean saccade frequency always a decrease of the width of the distribution of the saccade intervals has been observed which means that the occurrences of the saccades becomes more regular.

Gerrits and Vendrik (1974) used irregular saccade intervals in their experiments, the longer intervals were found to cause a complete disappearance of perception.

In figure 3.4 an example of our artificially generated saccade signals is shown. As in normal eye movements the horizontal and vertical components of the saccades occurred simultaneously.

In this example the frequency of the saccades was set to about 2 Hz. The mean and modal amplitude of the vectorial saccadic

displacements both measured 73 min.arc. The standard deviation measured 36 min.arc, while the maximal saccade magnitude occurring in a record which lasted 180 s measured 180 min.arc. From observed records we estimated the peak to peak amplitudes for the horizontal and vertical positions as 300 min.arc, each. The standard deviation of these horizontal positions and vertical positions measured 43 min.arc, each. The two noise signals which were used for the generation of the above described saccadic signals had been used as standard signals in the experiments. Its amplitude is signified with 1 AS (abbreviated from Artificial Saccade).

The size of these signals could be changed, while also the frequency of the saccades could be varied. In the experiments an extended range of saccade sizes and frequencies was studied.

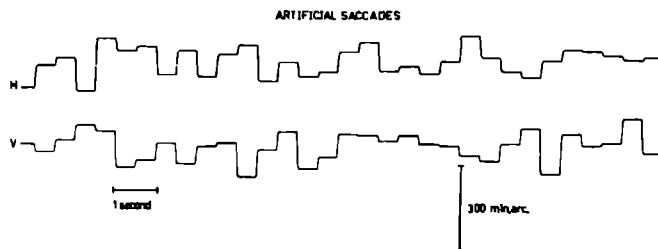


Fig.3.4 An example of the horizontal and vertical components of our artificially generated saccades. The amplitude measured 1 AS (see text), while the frequency of the saccades was 2 Hz.

The range of perception values obtained from the experiments in which the stimulus was moved by means of artificially generated saccades are illustrated in figures 3.5 and 3.6 for subject H.S. and H.G. respectively.

The artificial saccade amplitudes studied are 0.25 AS, 0.5 AS and 1.0 AS and the frequencies 1, 2, 3, 4 and 5 saccades per second.

As in the diagrams is indicated the quality of the perception increased with the movement amplitude. Also an increase of perception value was observed with the increase of the saccade

frequency up to about 3 Hz.

The indicated range of perceptions shows the fluctuating valuations of the subjects, mainly caused by the noisy character of the stimulus.

The influence of the retinal illumination level on the quality of the perceptions was studied for the different movement amplitudes at a saccade frequency of 2.5 saccades per second. The retinal illumination level had no observable influence on the quality of the perception for both subjects.

For subject H.G. besides the "older" measurements a number of outcomes is presented which were obtained from "newer" experiments in which the image sharpness and the condition of the subject's eye had better been controlled.

In all "newer" experiments and in many of the "older" measurements in which saccades of larger amplitudes (0.5 to 1.0 AS) were presented the subject complained about the reappearance of the thin black stalk with the fixation disk, positioned in the centre of the square (see General Method, section 3.2). In well stabilized condition this stalk should remain invisible after its initial fading. Its reappearance may be due either to destabilization (e.g. if the subject subconsciously follows the contour movement) or to activities generated when the large amplitude saccades occurred. These large saccades bring the fixation dot and the stalk near the border of the square or sometimes even outside the square where they become visible. Although the subject is uncertain whether he should or should not discard those measurements these outcomes are included in figure 3.6. In between the stimulus presentations the perception always disappears rapidly, i.e. when the square does not move for a short period of time.

3.5.3 The combination of artificial drifts and saccades: acquisition and use

We previously recorded and analysed the properties of the drifts and the saccades of both our subjects while they observed a square with sides of 4 degrees as a function of the brightness level and the given instruction (see chapter 1 - table IV and V).

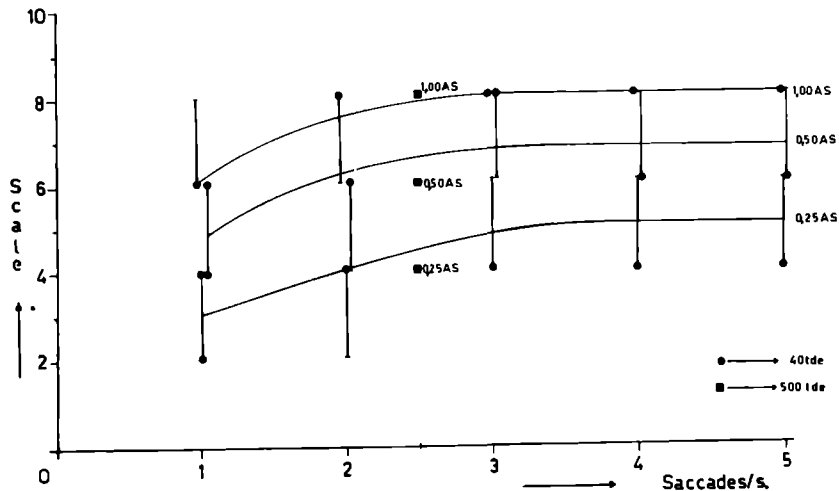


Fig.3.5 Perceptual value as a function of the amplitude and frequency of the artificial saccade movement and retinal illumination level; subject H.S.

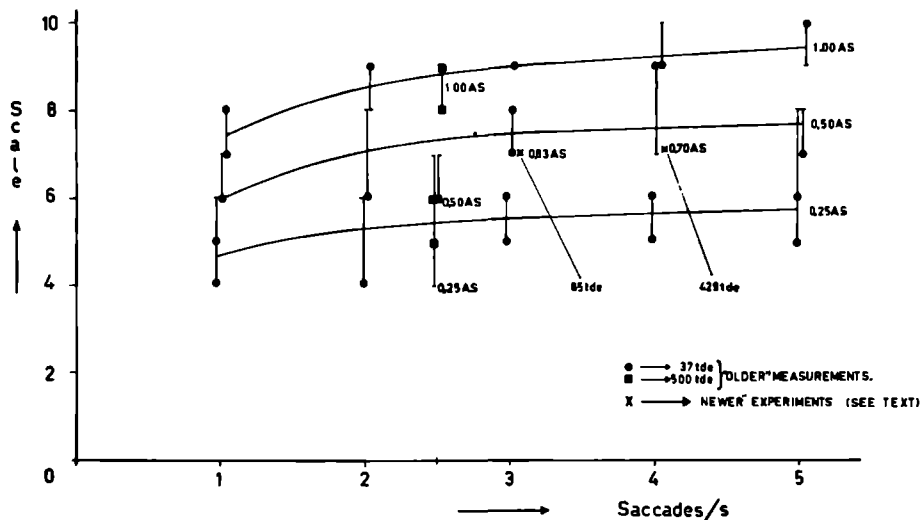


Fig.3.6 Perceptual value as a function of the amplitude and frequency of the artificial saccade movement and retinal illumination level; subject H.G.

Because of losses in the optic fibre, the artificial pupil and the limitation of the television monitor, the maximal retinal illumination amounted to about $550 \text{ td}_{\text{eff}}$ in our experimental set-up. Therefore the high retinal illumination levels as occurring during the observation of the square with a brightness of 150 cd/m^2 was unreachable in the experiments. We performed some experiments in which we combined artificially imitated drifts and saccades with properties as occurring during the observation of the square with a brightness of 5 cd/m^2 and 27 cd/m^2 for both subjects. In these experiments the retinal illumination was the same as during the measurements of the original eye movements (see chapter 1 table IV).

The artificial saccade magnitude used to imitate the real saccades was interpolated between the value that matched the mean vectorial saccade magnitude and the standard deviation σ of the previously recorded eye movements.

The saccade frequency was set to the mean value as occurring in the eye movements. For example see chapter 1 table V under Instruction 1 where the analysed properties of the eye movements are given of subject H.S. observing the stimulus with a brightness level of 5 cd/m^2 . The standard deviation measured 21.5 min.arc , the mean vectorial saccade magnitude was 49.2 min.arc , while the mean saccade frequency was 1.8 Hz . Matching the standard deviation results in an artificial saccade signal of 0.50 AS (divide 21.5 by 43). The match for the mean vectorial saccade magnitude results in an artificial saccade signal of 0.67 AS (divide 49.2 by 73).

As a compromise for the artificial saccade magnitude the average has been taken of 0.50 AS and 0.67 AS being 0.59 AS with a constant saccade frequency of 1.8 Hz .

There are indications that both the amplitude and the velocity of the drift movements are important. Therefore the amplitude of the artificial drift signals used to imitate the properties of the real drifts are interpolated between the value that matched the mean vectorial drift velocity and the mean vectorial drift magnitude as occurring in the eye movements. For matching the mean vectorial drift magnitude also the mean

saccade frequency is an important property. The measured mean vectorial drift magnitude of the artificial drift signal with an amplitude of 1 AD is given in figure 3.7 as a function of saccade frequency.

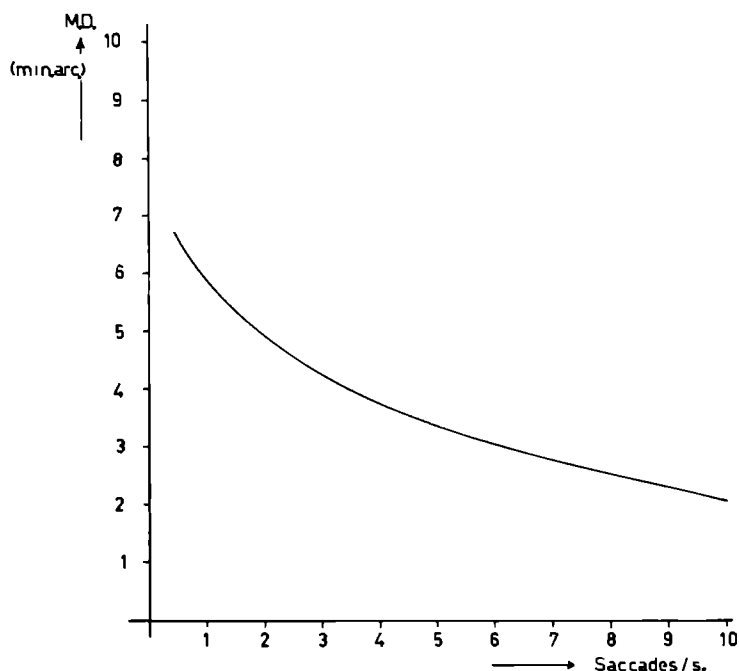


Fig.3.7 The measured mean vectorial drift magnitude (M.D.) as a function of the saccade frequency for a 1 AD magnitude artificial horizontal and vertical drift signal.

For example see again chapter 1 table V under Instruction 1 the analysed properties of the eye movements of subject H.S. observing the stimulus with a brightness level of 5 cd/m^2 . The mean vectorial drift velocity measured 24.0 min.arc/s , the mean vectorial drift magnitude was 10.1 min.arc , whereas the mean saccade frequency was 1.8 Hz . The match for the mean vectorial drift velocity results in an artificial drift signal of 1.1 AD (divide 24 by 21). In figure 3.7 we find a mean vectorial drift magnitude of 4.8 min.arc for a 1 AD signal with a constant saccade frequency of 1.8 Hz . The match on the basis of the mean

vectorial drift magnitude would thus result in 2.1 AD (divide 10.1 by 4.8). The mean of 1.1 AD and 2.1 AD, being 1.6 AD, has been taken as a compromise.

Table I shows the used combinations of the artificially generated drifts and saccades.

Table I. The combinations of artificially generated saccades and drifts calculated for the subjects H.G. and H.S.

Subject	H.G.		H.S.	
stimulus brightness and retinal illumination	5 cd/m ² 90 td _{eff}	27 cd/m ² 430 td _{eff}	5 cd/m ² 70 td _{eff}	27 cd/m ² 290 td _{eff}
Instruction I1			0.59 AS-1.8 Hz 1.6 AD	0.57 AS-2.1 Hz 1.8 AD
Instruction I2	0.61 AS-3.1 Hz 1.0 AD	0.63 AS-4.0 Hz 1.5 AD	0.97 AS-2.1 Hz 1.9 AD	0.81 AS-2.5 Hz 2.0 AD

Each subject studied the qualities of the perceptions when the square was moved with a combination of his imitated saccades and drifts. The obtained values of the perceptions can be compared with the perceptual quality obtained when the square moved with the artificial drifts or saccades only (values from figure 3.2 and 3.5 for subject H.S. and from figure 3.3 and 3.6 for subject H.G.). The results are represented in table II.

3.6 Formerly generated artificial eye movements

In foregoing experiments Gerrits and Vendrik (1974) investigated the efficiency of drifts and saccades (using the same experimental set-up and the same stimulus) by imitating the properties of eye movements as known from data available at that time.

They imitated the drift by using a Gaussian noise signal. Two uncorrelated signals (bandwidth 0 - 15 Hz) were recorded on two different channels of an instrumental tape recorder. By varying

Table II. The qualities of the perceptions obtained with the imitated eye movements with values expected according to the used instructions.

Subject instruc- tion	stimulus brightness (cd/m ²)	retinal illumination (td _{eff})	evaluation of the perception with:			expected value
			drifts only	saccades only	drift + saccades	
H.G. *	5	90	6	7	7	8
I2	27	430	7	7	7-8	8
H.S.	5	70	2-6	7-8	7-8	8
I2	27	290	2-6	7-8	7-8	8
H.S.	5	70	2-6	6	6	6
I1	27	290	2-6	6	6	6

* Scale values for drifts saccades, and both obtained in "newer" experiments. For subject H.S. the values for "drifts only" are obtained from the results as given in figure 3.2.

the recorder speed and the characteristics of RC- bandpass filters artificial drifts in the 0.12 - 1.5 Hz, 1.5 Hz - 5 Hz and 0.12 - 5 Hz bands were available. The peak to peak value was adjusted to about 30 min.arc amplitude by estimating this amplitude on the screen of an oscilloscope.

To imitate the microsaccades a binary noise signal was used which was adjusted to a constant amplitude of 30 min.arc and a clock period (i.e. a minimal interval time) either of 0.3 or 1.3 seconds.

Uncorrelated Gaussian noise signals (artificial drifts) and uncorrelated binary noise signals (artificial microsaccades) were combined to move the square in horizontal and vertical directions.

In two sessions we repeated their experiments copying their stimulus adjustments as well as possible. The different combinations of artificial drifts and saccades were presented in random order to subject H.G. and subject H.S. The outcomes

were practically equivalent to those described in the 1974 paper for subject H.G. However for subject H.S. the signal amplitudes needed to be increased by about a factor of 3 in order to generate a satisfactory percept (scale value of about 8).

3.7 Discussion

3.7.1 Our own results

The results shown in table II indicate that the imitation of the eye movements of subject H.S. under the instruction I1 generate percepts which meet the expected values fully, the other outcomes for both subjects are somewhat smaller than the expected values. Moreover it appears that the imitated saccades only provided the subjects with a perception of approximately the same quality as obtained during the unstablized observation of the same stimulus, which improved either nothing or a little by the addition of their drift movements. The effectiveness of drifts of physiological amplitude is larger for subject H.G. than for subject H.S., although the physiological drift amplitude of subject H.G. is smaller than of subject H.S. (table I). The percepts generated with only the saccadic movements are somewhat better for subject H.G. but much better for subject H.S. than those resulting from the drifts only. For subject H.G. the effectiveness of his saccades and drifts is about equal, whereas for subject H.S. saccades are more effective than his drifts. Both subjects found that the initial brightness of the square seen in experimental non-stabilized condition, i.e. when the square is observed through the free moving suction cap on the eye, decreased during the session. Moreover the originally bluish-white image always becomes somewhat yellowish in the course of time. The cause for this is unknown yet. In regard to the wearisome experimental procedures we conclude that there is no significant difference in the effectiveness of image movements in generating brightness under stabilized and unstabilized conditions. In general the tendencies observed in both subjects were very similar, increased movement sizes resulted in increased perception values for both subjects. However, with the same movement amplitudes subject H.G. observed a better stimulus quality than subject H.S. The fact that subject H.G. normally produced smaller eye movements than subject H.S. (see chapter 1, table V) was found in accordance with this result. Intersubject differences are well known in this kind of studies (King-Smith and Riggs, 1978).

We found that both subjects were very consistent in estimating their perceptual values, indicating that although there may be a difference between the subjects in the interpretation of the criteria in a given condition each subject was internally consistent in using his criteria.

Subject H.G. observed a better stimulus quality with higher retinal illumination levels for the drift movements, while subject H.S. could not observe any difference. This can not be explained yet. For the saccades both subjects observed no remarkable differences for the different brightness levels. In the experiments the stimulus-background contrast, defined as $(B_{\max} - B_{\min}) / (B_{\max} + B_{\min})$, was constant (0.96). In a few pilot experiments subject H.G. found lower evaluations when the contrast was decreased.

3.7.2 Comparison with the results of Gerrits and Vendrik (1974)

As described in section 3.6 we repeated their experiments in two sessions. An accurate comparison of their outcomes with our results is difficult as at that time a somewhat different scale to describe the perceptions was used. Moreover, their movement signals had different spatial and spectral characteristics, especially their saccade signal is very different from ours. They concluded that the irregularity (defined as the continuous change of the direction) and the continuity of the movement (defined as the movement velocity at any moment which has to exceed a certain lower limit) were the important properties for the preservation of the perception.

We feel that irregularity, which we would define as randomly distributed positions of the image within a certain area large enough to prevent spatial adaptation (Blakemore and Campbell, 1969; Campbell and Robson, 1961) is an important property. In contrast our experiments with saccades alone showed that continuity of the movement is not an absolute necessity for the generation and preservation of a perception of brightness. We proved (see figures 3.2; 3.3; 3.5 and 3.6) that drifts or saccades alone, if only of greater amplitude than physiologically present, can generate a satisfactory percept.

3.7.3 The efficiency of drifts and saccades as a function of the stimulus size

Fading of the perception of peripherally located stimuli by accurate fixation of a spot has previously been described by Troxler (1804) and Clarke (1957). When subject H.S. suppressed his eye movements during the normal observation of a bright square with sides of 4 degrees this also resulted in a complete fading of the perception within a short time. According to Carpenter (1977) this result can be obtained by subjects who are able to exercise control over their microsaccades. After a short time of steady staring the vision in the periphery of the field begins to blur and mist over and after a time this appearance begins to invade the fovea.

The fading of the perception of a square with sides of 4 degrees observed with suppressed eye movements indicates a totally insufficient effectiveness of the remaining drift movement. Probably the suppression of the saccades also resulted in a reduced size of the remaining drifts, as the normal drifts for subject H.S. would generate a perception value between 2 and 6 (see table II). In contrast when subject H.S. suppressed his saccades during the observation of a small square, e.g. one with sides of 15 min.arc., this always resulted in the maintenance of a normal perception of that particular square. From this result we might conclude that the drifts are sufficient to elicit a normal continuous perception for small objects in and probably also around the fovea. Because there is no difference in perception of brightness during normal fixation of small targets with or without the small saccades these saccades seem to play a minor role during foveal brightness observation.

Steinman et al. (1967) also demonstrated the minor importance of microsaccades during maintained monocular fixation.

3.7.4 Comparable data from the literature

As far as we know no other investigation has been carried out concerning the efficiency of drifts and saccades for the brightness perception of homogeneous fields of various sizes,

i.e. the goal we set ourselves.

Imitation of eye movements has been performed besides in these experiments and those of Gerrits and Vendrik (1974) only by Sharpe (1972). He imitated the properties of fixational eye movements for visualizing the shadows of the retinal blood vessels. As the fading of those shadows was found to be orientation and width specific Sharpe concluded that the required type of eye movement must distribute the excitation over as many different orientation and spatial frequency channels as possible (see also Blakemore and Campbell, 1969; Campbell and Robson, 1968). He accomplished this by varying the direction and the velocity of image movement as in normal eye movements. For the imitation of the fixational eye movements he generated the movement of a spot starting from the centre of the pupil with a small series of steps executing a first-order pseudo random walk followed by a jump back to the centre of the pupil. The small steps measured 0.2 min.arc and were intended to imitate the properties of the tremor in eye movements (Ratliff and Riggs, 1950). The drift component was composed of the series of steps, while the jump back to the centre of the pupil corresponded to the saccade. Since the amplitude of the saccades studied in his experiments measured only 0.2, 1.7 and 2.0 min.arc, which was quite small compared to the used previous drift movement this might explain why the image movement incorporating this small final saccade was found no more effective in producing perception than the movements lacking the saccade.

Sharpe emphasized the importance of larger voluntary saccades in order to prevent spatial adaptation. He assumed the apparent contrast of the visual scene to decrease by spatial adaptation. Changing the fixation point will limit this process by shifting spatial frequency harmonics and orientations to regions of the visual field unadapted to these specific features.

Sharpe never succeeded to preserve perception of the shadows and attributed this to the low contrast and small movement amplitudes used in his experiments. Drysdale (1975) who used larger amplitudes found longer visibility times for these larger movements, again indicating the role of the size of the movements for the prevention of adaptation which resulted in a longer

visibility time. Other experimenters investigated the effectiveness of regular v. irregular movements for the perception of a stabilized stimulus.

As has been previously mentioned (3.7.2) Gerrits and Vendrik (1974) came to the conclusion that irregularity of the eye movements is an important property for the preservation of the perception. We agree with this conclusion under our new definition of irregularity. Results reported in the literature show that regular movements, even of larger amplitudes, may easily lead to spatial adaption (Blakemore and Campbell, 1969; Campbell and Robson, 1961). A number of examples of this spatial adaption (habituation) for rotational as well as for square wave movements can be found in the reports of Ditchburn et al. (1959) and Gerrits and Vendrik (1970a; 1974). From their outcomes as well as from the work of Sharpe (1972) and Drysdale (1975) it can be concluded that the effectiveness of regular movements on the perception depends also on the amplitude. For instance Drysdale showed that for an amplitude of a circular motion which was estimated to correspond to 30 min.arc in diameter at the retina the visibility of the retinal blood vessels (defined as the percentage of time during which the retinal blood vessels were observable) was found to exceed 50 per cent for frequencies in the range of 0.5 - 4 Hz. When the amplitude was reduced to 60 per cent this visibility never exceeded 20 per cent even for corresponding velocities. Optimum velocities were about 1.5 degrees/s (Drysdale) and about 2 degrees/s (Sharpe). A rough comparison of these optimum velocities with velocities occurring in our artificial drift signal results in matches of 4.3 and 5.7 AD respectively, giving perception 6 or more according to figures 3.2 and 3.3.

Recently King-Smith (1978) proposed a semiquantitative model consisting of a spatial filter followed by a temporal filter which was used to explain why visual sensitivity to optimal square wave movement was markedly smaller than to optimum triangular movement. She also indicated that under normal viewing conditions it is unlikely that the stimulus (a line stimulus was studied) would remain in one region of the spatial filter for long enough time to cause much depression.

According to the model equally sized saccades and drifts would generate responses in the pattern system which are of comparable size.

A rough comparison of the perception values obtained with artificial saccade amplitudes of 0.25 AS; 0.50 AS and 1.0 AS at a frequency of 2.5 Hz with those of artificial drift amplitudes of corresponding size (standard deviation) being 1.7 AD; 3.4 AD and 6.8 AD, respectively, in figures 3.2 and 3.5 for subject H.S. and in figures 3.3 and 3.6 for subject H.S. also indicates similar outcomes.

3.7.5 A view on the role of the drifts and the saccades

Recently Gerrits (1978) showed that the foveal parts of a stabilized image fades much faster (i.e. in a few hundred milliseconds) than the more peripheral parts which need a few seconds to disappear. Moreover, the foveal area of the retina could be activated by smaller amplitude movements than the more peripheral retinal areas. When the fovea is located in the centre of a larger homogeneous field the rapid fading of its activity is not observed because the filling-in homogenizes the field with activities generated in the periphery.

In our experiments the fovea was positioned initially in the centre of the square (4 by 4 degrees) and the movement started only after the complete fading of the square, i.e. after that only a faint diffuse brightness was left.

The saccadic components of the artificial movements shift the stimulus to "fresh" areas of the retina, enabling the cells present there to signal "light-on" to the brain. The peripheral visual field seems to benefit particularly from larger saccades because the brightness-generating effectiveness of the drift movements decreases rapidly in the periphery. The filling-in mechanism, the spread of newly generated activities towards non-reactivated areas, is thought to provide for the perception of brightness for the whole square (Gerrits and Vendrik, 1970 b). Starting from a completely faded image both subjects needed about 20 to 30 seconds before the centre of the moving square had acquired its final brightness level which, however, still

fluctuated in the course of time. The fluctuations are, according to the subjects, strongly correlated with the noisy character of the stimulus movement, but fluctuating sensitivity of subjects can not be excluded completely as an additional cause.

In the experiments described in this chapter as well in former experiments subject H.G. observed that in first instance the strongest contribution of brightness to homogenize the square did not come from the on-border but from the inside of the square. Just after the beginning of the movement the subject observed two bright on-borders (indicated below as movement on-borders) and two dark off-borders (called movement off-borders) which enclosed the remaining part of the square not falling on new retinal receptors. This "midpart", i.e. the part situated in between these movement on- and off-borders, was not homogeneous. Brightness was generated on this midpart just beyond the movement off-border and this induced brightness spread in the direction of the bright movement on-border. Likewise darkness was generated on this midpart just beyond the movement on-border and this induced darkness spread towards the dark movement off-border. The brightness and darkness spreading from these two induced activities met somewhere in the centre of the midpart. As a result this raised for subject H.G. the impression of triangles continuously changing their orientation when the square moved in another direction (see also section 3.5).

The generation of this induced brightness and darkness activity can be fully explained by the well-accepted correlating activities of on-center cells and off-center cells darkened and illuminated respectively in their antagonistic receptive field surrounds. These induced activities have been observed by subjects L.v.E. and H.G. in several similar stimuli in stabilized condition. They are also visible in normal vision, although in much weaker form, and are known as Mach bands.

The induced darkness activity generated along the movement on-border either functions as a barrier against the spread of brightness from the movement on-border to the midpart of the square or diminishes strongly the brightness trying to reach the midpart by spread. Whatever theory is correct as a result the part situated along the movement on-border looks considerably darker than

along the off-border. In the course of time the inhomogeneity seen at first in the midpart as a result of two opposite induced activities diminishes, the difference between the movement on-border and the midpart becomes smaller. Also the contour between the movement on-border and the midpart, being sharp at the start of the movement, shallows more and more during continued stimulation. However, even after a long time of movement the midpart remains darker than the movement on-border but the movement off-border disappears.

An additional effect of the saccadic movements was mentioned by subject H.G. According to this subject in normal vision the fovea does not remain near the centre of the square but jumps around the contours and even occasionally outside the square. Most saccadic movements will not only displace the image to activate many receptors situated in the retinal periphery but will also bring the fovea along different parts of the contours. The drift, continuously moving the stimulus in between the saccades, is very effective to generate brightness when the contour is located near the fovea. The task of the saccades for generation brightness is, therefore, twofold: to refresh the activities in the retinal periphery and to enable the drift to generate brightness in the foveal area.

If this reasoning is correct what changes in the saccade and drift properties should be expected when the size of the square increases? The saccade amplitudes should increase accordingly in order to execute its double task. There is no need for the drift amplitude to increase because the fovea is transferred (by the saccades) close to the contours where the drifts are always very effective.

The results described in chapter 1 show that indeed the increase in eye movement amplitudes with increasing square size are mainly brought about by the saccades, while changes in the drifts seem to play a minor role (see section 1.4.1).

New experiments are needed to verify this hypothesis about the task of the saccades for the generation of brightness and darkness in normal vision.

Finally another difference between the eye movements in our experiments and those in normal vision has to be considered.

In normal vision head movements, as far as these are not compensated by the vestibular system, seem to contribute considerably to the movements of the image over the retina. This is found recently by Skavenski et al. (1979) and Steinman and Collewyn (1980). It should be expected therefore that a subject with a clamped head, as in our experiments, needs to exaggerate his eye movements with respect to normal vision if he faithfully follows the instruction to provide for a normal image of the stimulus. If the subject is unable to adjust his eye movements to meet this criterium a percept of lower quality should be expected. In view of the data about the importances of head movements in normal vision it seems necessary to study eye movements with a free moving head in future experiments.

3.8 References.

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Samenvatting.

Dit proefschrift beschrijft de nauwkeurige meting en analyse van oogbewegingen met een onderzoek naar hun betekenis voor de visuele perceptie, in het bijzonder de perceptie van helderheid. In hoofdstuk I worden naast de gebruikte meetmethode en analysetechniek de opgemeten oogbewegingen gedurende het kijken naar vierkante vlakken van verschillende afmetingen beschreven voor meerdere proefpersonen. De verkregen resultaten tonen aan dat de grootte van de oogbewegingen toeneemt met de grootte van het vlak waarnaar wordt gekeken. Deze toename wordt hoofdzakelijk veroorzaakt door een toename van saccade amplitudes en frequenties, terwijl de veranderingen van de drift bewegingen gering zijn. Om deze reden blijkt een kleinere rol voor de drifts bij de perceptie van helderheid in grotere vlakken.

In hoofdstuk II worden de oogbewegingen opgemeten gedurende binoculaire fixatie op een klein vlakje beschreven. In de opgemeten oogbewegingen is een sterke correlatie gevonden voor zowel de saccades als de drifts in de beide ogen. Dit gegeven toont aan dat saccades en drifts onder controle staan van een voor beide ogen gemeenschappelijk stuurcentrum.

In hoofdstuk III worden de onderzoeken naar de invloeden van retinale beeldbewegingen voor de perceptie beschreven. Met behulp van een stabilisatietechniek is de invloed van de momentane oogbewegingen gedurende de experimenten uitgesloten.

De invloed van saccades en drifts is zowel afzonderlijk als in combinatie onderzocht voor een vierkant helder vlak met zijden van vier graden. De resultaten tonen aan dat de beide proefpersonen met hun saccades een helderheidsperceptie krijgen die ongeveer hetzelfde is als gedurende het ongestabiliseerd kijken naar deze stimulus. Door de toevoeging van hun drifts verbeterde de helderheidsperceptie nauwelijks. Voor de efficiëncy van hun drifts is een opmerkelijk verschil tussen de beide proefpersonen gevonden. Ondanks het feit dat de drifts van proefpersoon H.G. aanzienlijk kleiner zijn dan die van proefpersoon H.S. ziet proefpersoon H.G. hiermee een betere beeldkwaliteit dan proefpersoon H.S. met zijn grotere drifts.

Voor proefpersoon H.G. is de efficiëncy van zijn saccades en

drifts ongeveer gelijk, voor proefpersoon H.S. daarentegen zijn saccades veel efficiënter dan de drifts.

Uit de verrichte experimenten en literatuurgegevens blijkt dat drifts voldoende zijn voor het handhaven van foveale helderheidspercepten. Vanwege de lage frequenties waarmee de kleine saccades in de oogbewegingen gedurende foveale fixatie voorkomen zijn deze ongeschikt voor het handhaven van een foveale helderheidsperceptie.

Voor foveaal waarnemen van kleine voorwerpen voldoen de drifts, voor grote voorwerpen voldoen de saccades, terwijl voor de daartussen liggende grootten saccades en drifts samen bijdragen voor het handhaven van de helderheidsperceptie.

Henk Stassen werd op 1 januari 1949 geboren te Stevensweert. In 1966 behaalde hij het diploma HBS-B aan het Bisschoppelijk College te Roermond, waarna hij begon met een opleiding in de technische natuurkunde aan de Technische Hogeschool te Eindhoven. In 1972 behaalde hij zijn ingenieursexamen en de onderwijsbevoegdheid voor natuurkunde en mechanica. Het afstudeerwerk werd verricht in de sectie Biomechanica en Medische Instrumentatie van de afdeling der werktuigbouwkunde. Een methode voor het meten van dynamische spierkrachten werd ontwikkeld en getest (coach Dr. Ir. C.J.Snijders, afstudeerhoogleraren Prof. Ir. A.Horowitz en Prof. Dr. P.v.d.Leeden). Na zijn afstuderen was hij nog enkele maanden werkzaam als adjunct wetenschappelijk medewerker bij de sectie Biomechanica en Medische Instrumentatie. Van maart 1973 tot juli 1973 was hij werkzaam als leraar natuurkunde aan de R.K.S.G. Sintermeerten te Heerlen. Vanaf augustus 1973 tot juni 1978 is hij in dienst geweest van de Katholieke Universiteit te Nijmegen om op het Laboratorium voor Medische Fysica en Biofysica zijn in dit proefschrift beschreven onderzoek te verrichten. In 1979 was hij werkzaam op de Erasmus Universiteit te Rotterdam op het Instituut voor Keel-, Neus- en Oorheelkunde, waar voor het vestibulaire systeem van de mens drempels voor rotatoire bewegingen om de verticale as werden gemeten (projectleider Dr.M.Rodenburg). Tevens behaalde hij in 1979 aan de Hogere Technische School te Rotterdam de examens verbonden aan de Applicatiecursus Ioniserende Straling B en C. Vanaf november 1979 is hij als leraar benoemd aan de R.K.S.G. "Stella Maris" te Meerssen. In zijn vrije tijd is hij een actief "doe het zelfver", in het bijzonder de restauratie van enige klassieke engelse automobielen is zijn hobby.

STELLINGEN

1. Het veelal gevonden verschijnsel dat foveale percepten langzamer wegzakken dan periphere percepten is het gevolg van onvoldoende stabilisatie van het retinale beeld.
Gerrits, H.J.M. Differences in peripheral and foveal effects observed in stabilized vision. Exp. Brain Research 32, 225-244 (1978).
2. Het optreden van overshoots bij kleine saccades is persoonsafhankelijk.
Dit proefschrift.
3. Het regelmatig uitvoeren van stabilisatie-experimenten dient gepaard te gaan met een regelmatig oogonderzoek.
4. Door het logaritmisch uitzetten van de psychometrische curve voor de rotatiedrempels van het vestibulaire systeem ontstaan curves die grote overeenkomsten vertonen met de psychometrische curves voor het auditieve en het visuele systeem.
Rodenburg, M., Maas, A.J.J. and Stassen, H.P.W. Thresholds for rotation: variability, psychometric curves and comparison with hearing thresholds. Internal report, Department of Otorhinolaryngology, Erasmus University Rotterdam (1980).
5. Het opmerkelijke verschil in de beschreven effecten van Lycopodium in de farmacologische literatuur enerzijds en de homeopathische literatuur anderzijds verdient een nader onderzoek.
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A dictionary of practical materia medica by John Henry Clarke, M.D. Volume II, Iberis-Pelargonium Reniforme, Health Science Press, Bradford Holsworthy, Devon (1977).
6. Het nog slechts in zeer geringe mate gebruik maken van schoolmeubilair dat is voorzien van de mogelijkheid om mee te groeien met de leerling vormt een bedreiging voor de volksgezondheid.
7. Het aanbod van educatieve programma's door de Belgische Radio en Televisie en de West Deutscher Rundfunk lijkt meer afgestemd op de leerplannen van het voortgezet onderwijs in Nederland dan het aanbod van T.V. programma's door de Nederlandse Onderwijs Televisie.
8. Het veranderen van agrarische gebieden in waterplassen als gevolg van ontgrindingen dient gepaard te gaan met een gepaste omscholing voor de betrokken agrariërs.
9. In het belang van de antieke auto is het wenselijk hiervoor ook de antieke motorrijtuigenbelasting tarieven te hanteren.

